PHILOSOPHICAL TRANSACTIONS

OF THE

ROYAL SOCIETY OF LONDON.

VOL. 178 (1887), B, pp. 5–37.

[PLATES 2–5.]

REMARKS

ON

THE CLOACA AND ON THE COPULATORY ORGANS OF THE AMNIOTA.

BY

HANS GADOW, PH.D., M.A.,

LECTURER ON THE ADVANCED MORPHOLOGY OF VERTEBRATA, AND STRICKLAND CURATOR IN THE UNIVERSITY OF CAMBRIDGE.

LONDON:

PUBLISHED FOR THE ROYAL SOCIETY

BY TRÜBNER AND CO., LUDGATE HILL, E.C.

1887.

Price Three Shillings and Sixpence.

II. *Remarks on the Cloaca and on the Copulatory Organs of the Amniota.*

By Hans Gadow, *Ph.D., M.A., Lecturer on the advanced Morphology of Vertebrata, and Strickland Curator in the University of Cambridge.*

Communicated by Professor M. Foster, *Sec. R. S.*

Received March 11,—Read March 25, 1886.

[Plates 2–5.]

Contents.

PAGE.

Chapter I.—Muscles of the Cloaca 9
Muscles of the Cloaca of the Crocodilia 10
Cloacal and copulatory muscles of Chelonia 10
„ „ Birds 11
„ „ Sauria 12
„ „ Hatteria 12
„ „ Mammalia 12
Chapter II.—The nerve-supply of the Cloacal region in Crocodiles 14
Chapter III.—The modifications of the Cloaca 15
Crocodilia 16
Sauria 18
Ophidia 18
Hatteria 19
Aves 20
Chelonia 21
Anal pouches 22
Peritoneal canals 23
Monotremata 26
Marsupialia 26
Placentalia 27
Summary of Chapter III. 28
Chapter IV.—On the presence of Müllerian ducts in the males, and of Wolffian ducts in the females of young Crocodilia 30
Chapter V.—General conclusions 30–32

A rich material of Crocodiles and Alligators has enabled me to clear up several points in the structure of their sexual apparatus, which have hitherto escaped notice, probably owing to the scarcity of suitable specimens. This latter difficulty has been removed in my case by the liberality of the University of Cambridge and of the Royal Society, which has enabled me, in conjunction with Dr. Gaskell, to

construct a special house to keep alive, and in a healthy condition, a considerable number of Reptiles of all orders.

The study of fresh material possesses great advantages over that of preserved and diseased specimens, especially though if the anatomical results can be checked by observation of the functions of the organs.

For a specimen of Siphonops annulatus I am indebted to Dr. A. Günther, for some of the Alligator embryos to Professor W. K. Parker. Struthio embryos had been collected by Mr. Sedgwick, aided by a grant from the Royal Society. Several well-preserved Ornithorhynchus and Echidna Mr. Sedgwick kindly put at my disposal. Adult specimens of Struthio, Rhea, Casuarius, and Apteryx belonged to the museum of the University of Cambridge, and came for the most part from the Zoological Garden, in London. In connexion with these investigations turned up several questions concerning the Cloaca, which suggested a comparative treatment of the whole cloacal region and of the copulatory organs throughout the Amniota.

Of Reptiles the following material was at my disposal :—

*Alligator mississipiensis. Several embryos and several fresh specimens of about 5 feet in length.
Crocodilus palustris. Several baby specimens.
Crocodilus acutus. About 3 feet long.
*Crocodilus biporcatus. Numerous fresh specimens from 8 inches to 24 inches in length. One specimen of about 3 feet.
Crocodilus vulgaris. Male copulatory organ of adult; specimen in R.C.S.
Crocodilus sp. ? Half adult female; preparation in the Cambridge Museum.
Monitor indicus.
*Lacerta ocellata. Numerous specimens.
*Lacerta viridis. Numerous specimens.
Psammosaurus scincus.
*Hatteria punctata. Male and female.
*Tropidonotus natrix. Numerous specimens.
Pelophilus madagascariensis. Male and female.
*Testudo græca.
*Emys europæa.
*Clemmys caspica. } Numerous specimens.

There is an abundant literature on this subject, but the descriptions and conclusions found in it frequently agree neither with each other nor with the actual facts. A discussing review of the literature would lie beyond the scope of this paper. I append, however, a list of the papers which I have consulted..

* The species marked with an asterisk were, or are, kept in the Reptile-house.

ALESI, VINCENZO. "Sulla borsa di Fabricio negli uccelli." 'Milano, Soc. Ital. Atti,' vol. 18, 1875, pp. 133–169 ; plates 4 and 5.

ANDERSON, JOHN. "On the cloacal bladders and on the peritoneal canals in Chelonia." 'Linn. Soc. Journ. (Zool.),' vol. 12, 1876, pp. 434–444.

BARKOW, H. "Von der Kloake verschiedener Vögel." 'MECKEL, Archiv,' 1829, pp. 443 *et seq.* ; plates 9 and 10.

BERTHOLD, A. A. "Ueber den Fabricischen Beutel der Vögel." 'Acad. Cæs. Leopold. Nova Acta,' vol. 14, 1828, pp. 903–918.

BOJANUS. 'Anatome Testudinis europææ.' Vilnæ, 1819–21 ; plate 30.

BORNHAUPT, TH. 'Untersuchungen über die Entwicklung des Urogenitalsystems beim Hühnchen.—Dissert. inaug.' Riga, 1867.

BRIDGE, T. W. "Pori abdominales of Vertebrata." 'Journ. Anat. Physiol.,' vol. 14, 1879 [1880], pp. 81–100.

BUDGE, J. "Ueber das Harnreservoir der Wirbelthiere." 'Greifswald, Naturw. Ver. Mittheil.,' Heft 7, 1876 (3 plates).

DUMÉRIL et BIBRON. 'Erpétologie générale.'

DUVERNOY, G. L. "Fragment d'anatomie comparée sur les organes de la génération de l'Ornithorhynque et de l'Échidné." [1830.] 'Strasbourg, Soc. Hist. Nat. Mém.,' vol. 1 (2e Livr.), Mém. I.

DUVERNOY (CUVIER). 'Leçons d'Anatomie comparée.' 2nd edition. Vol. 7, 1840.

FORBES, W. A. "On the bursa Fabricii in birds." 'Zool. Soc. Proc.,' 1877, pp. 304–318.

FRITSCH, A. "Zur Anatomie der Elephanten-Schildkröte." [1870.] 'Prag, Abhandl.,' vol. 4.

GADOW, H. "Beiträge zur Myologie der hinteren Extremität der Reptilien." 'Morphol. Jahrb.,' vol. 7, 1882, pp. 329–466 ; plates 17–21.

GASSER, E. 'Beiträge zur Entwicklungsgeschichte der Allantois, der Müller'schen Gänge und des Afters.' Frankfurt a/M., 1873. (3 plates.)

"Die Entstehung der Cloakenöffnung bei Hühnerembryonen." 'Archiv Anat. Physiol. (Anatom. Abthg.),' 1880, pp. 297–319 ; plates 12 and 13.

GEOFFROY-SAINT-HILAIRE, ÉTIENNE. "Considérations générales sur les organes sexuels des animaux à grandes respiration et circulation." [1823.] 'Paris, Mus. Hist. Nat. Mém.,' vol. 9, pp. 393–412.

"Composition des appareils génitaux, urinaires et intestinaux, à leurs points de rencontre dans l'autruche et dans le casoar." *Ibid.*, vol. 9, pp. 438–456 ; plate 21.

"Sur les appareils sexuels et urinaires de l'Ornithorhynque." *Ibid.*, vol. 15, 1827, pp. 1–48 ; plates 1 and 2.

'Philosophie Anatomique.—(Vol. 2.) Des Monstruosités humaines.' Paris, 1822. (Plate 17 contains figures of the cloaca of the turkey, fowl, duck, and peacock.)

Geoffroy-Saint-Hilaire, Isidore, et Martin-Saint-Ange, G. J. "Recherches anatomiques sur deux canaux qui mettent la cavité du péritoine en communication avec les corps caverneux chez la tortue femelle, et sur leurs analogues chez le crocodile ; et remarques sur la structure et la disposition du cloaque, du clitoris et des corps caverneux chez la tortue." 'Ann. Sci. Nat.,' vol. 13, 1828, pp. 153–201 ; plates 6 and 7.

"Note sur les canaux péritonéaux des Emydes et du crocodile, mâles." *Ibid.*, vol. 13, 1828, pp. 201–204, 447–449.

Günther, A. "Contribution to the anatomy of Hatteria (Rhynchocephalus, Owen)." [1867.] 'Phil. Trans.,' vol. 157, pp. 595–629 ; plates 26–28.

Huschke, E. 'De Bursæ Fabricii Origine.' Jenæ, 1838. (With plate.)

Kobelt, G. L. 'Die männlichen und weiblichen Wollust-Organe des Menschen und einiger Säugethiere.' Freiburg i. B., 1844.

Lataste, F. "Injection des canaux péritonéaux chez la Testudo nemoralis." 'Journ. de Zool.,' vol. 6, 1877, p. 389.

Lereboullet. "Recherches sur l'anatomie des organes génitaux des animaux vertébrés." [1848.] 'Acad. Cæs. Leopold. Nova Acta,' vol. 23, 1851, pp. 1–228.

Lesueur. "Sur deux vessies auxiliaires dans les tortues du genre Emys." 'Comptes Rendus,' vol. 9, 1839, pp. 456–457.

Leydig, F. 'Die in Deutschland lebenden Arten der Saurier.' Tübingen, 1872.

Martin-Saint-Ange. 'Étude de l'Appareil reproducteur dans les cinq Classes d'Animaux vertébrés.' Paris, 1856.

Mayer, A. F. J. C. 'Analecten für vergleichende Anatomie.' Bonn, 1835. (Plate 3, fig. 9—male organ of Chelone midas.)

"Appareil génito-urinaire des oiseaux." Abstract in 'L'Institut,' vol. 9, 1841, p. 231 ; and 'Neue Untersuchungen a. d. Gebiete der Anat. und Physiol.,' Bonn, 1842.

Meckel, J. F. (Jun.). 'Ornithorhynchi paradoxi Descriptio anatomica.' Lipsiæ, 1826 ; plates 5, 7, and 8.

Müller, J. 'Bildungsgeschichte der Genitalien.' Düsseldorf, 1830.

"Ueber zwei verschiedene Typen in dem Bau der erectilen männlichen Geschlechtsorgane bei den straussartigen Vögeln, und über die Entwickelungsformen dieser Organe unter den Wirbelthieren überhaupt." 'Berlin, Abhandl.,' 1836. (With 3 plates.)

Owen, R. "On the anatomy of Crocodilus acutus, Cuv." 'Zool. Soc. Proc.,' Part I., 1830–31, pp. 139–141.

RATHKE, H. 'Entwickelungsgeschichte der Natter.' Königsberg, 1839. (With 7 plates.)

'Entwickelungsgeschichte der Schildkröten.' Braunschweig, 1848. (With 10 plates.)

'Untersuchungen über die Entwickelung und den Körperbau der Krokodile.' Braunschweig, 1866. (With 10 plates.)

RETTERER, ÉD. "Contribution à l'étude du cloaque et de la bourse de Fabricius chez les oiseaux." 'Robin, Journ. Anat. Physiol.,' Année 21, 1885, pp. 369–454; plates 17–19.

SPANGENBERG. 'Disquisitio circa Partes genitales fœmineas Avium.' Gottingæ, 1813.

STANNIUS, H. 'Zootomie der Amphibien.' 2nd edition. Berlin, 1856.

TANNENBERG. 'Circa Partes genitales masculas Avium, disq. anatom.' Gottingæ, 1789.

'Abhandlung über die männlichen Zeugungstheile der Vögel.' Göttingen, 1810. (With plates.)

TOWNSON. 'Observationes physiologicæ de Amphibiis.—Fragmentum de Absorptione.' Gottingæ, 1795.

TREVIRANUS, G. R. "Ueber die Harnwerkzeuge und die männlichen Zeugungstheile der Schildkröten überhaupt und besonders der Emys serrata." 'TIEDEMANN, Zeitschrift,' vol. 2, 1827, pp. 282–288; plate 13.

WAGNER, RUDOLPH. "Beiträge zur Anatomie der Vögel." 'München, Abhandl.,' vol. 2, 1837, pp. 271–308. (With plate.)

WIJHE, J. W. VAN. "Bijdrage tot de kennis van het urogenitaal-system bij de schildpadden." 'Nederl. Dierk. Vereen. Tijdschr.,' vol. 5, 1880.

Of text-books, see BALFOUR, BRONN-HOFFMANN, CUVIER, GEGENBAUR, HUXLEY, MECKEL, MILNE EDWARDS, STANNIUS, TIEDEMANN, and WIEDERSHEIM.

I. *Muscles of the Cloaca.*

Crocodilia (figs. 3, 5, 8, 9).—After removal of the skin appears on each side of the anal opening a continuation of the M. rectus abdominis lateralis, which, a little beyond the caudal corner of the opening, is attached to the M. ilio-ischio-caudalis, the chief mass of the lateri-ventral muscles of the tail.

Partly covered and crossed by the M. rectus lateralis is the M. transversus perinei, which, enclosed between the rectus lateralis and the ischiadic portion of the lateral tail muscle, arises from the first processus transversi of the caudal vertebræ as a thin semi-aponeurotic plate, gradually thickens, and is inserted with transversely running

fibres on to the caudal end of the Symphysis ischii and to the neighbouring corner of the anal opening. Contraction of this muscle opens the anus.

The side walls of the anal portion of the cloaca are surrounded by a rather thin layer of muscles, which arise in the median line between the right and left halves of the M. ischio-caudalis, from some of the first chevron bones of the caudal vertebræ. Their fibres are directed more or less transversely towards the margin of the anus, where they are attached. The most superficial portion of this system has, however, a more longitudinal direction and is somewhat differentiated off from the rest; its fibres meet at the anterior corner of the anus and surround the latter like a sphincter. Their contraction closes and elongates the anal slit, whilst through the action of the more transverse, deeper mass the anal walls are drawn inwards and are thus likewise closed.

All these muscles, viz., the M. transversus perinei, *s.* transversus lateralis, *s.* levator, and the M. transversus medianus, *s.* sphincter, together with the M. rectus lateralis, are supplied by a strong branch of the ischiadic plexus. In *Alligator mississipiensis* this nerve-branch comes from the stem α, *i.e.*, the first postsacral spinal nerve. It leaves the pelvis laterally from the tendinous insertion of the M. ischio-caudalis, between this tendon and the posterior margin of the ischium near the symphysis, and then it supplies, situated superficially, the muscles, sending out at the same time cutaneous branches.

Considering the nerve-supply, it seems more reasonable to suppose that the sphincter muscles are, at least in the Crocodilia, a differentiation of the post-pelvic portion of the system of the M. rectus abdominis, and not of the true caudal muscles.

In the *Chelonia* the penis is not attached to the pelvis, nor is it in connexion with any anal muscles; but to its dorsum, not far from the glans, are attached a pair of long retractor muscles, which pass laterally from the M. pubi-caudalis (fig. 10) (flexor caudæ obturatorius, Bojanus) into the pelvis, and arise from one of the most anterior lumbar vertebræ. The position and nerve-supply of these peculiar muscles show that they are differentiated from the MM. lumbo-caudales (flex. caudæ lumbales, Bojanus). There is consequently no homology whatever between this Chelonian retractor (sometimes called M. ischio-cavernosus) and any of the Avian and Mammalian copulatory muscles. Its function is somewhat complicated. When the penis is erected and protruded, the muscle acts as the retractor, but when the organ is in a relaxed condition and, when at rest, doubled up and withdrawn into the cloaca, as shown in fig. 26, contraction of the muscle, owing to its pulley-like course round the M. pubi-caudalis, undoubles it and protrudes it so far that the glans becomes visible in the anal opening. This is seen in micturating Tortoises, because the penis has to be straightened in order to withdraw the glans from its position ventrally from the fold *p*, where it blocks the opening of the bladder. During defæcation, on the other hand, the doubled halves of the penis are pressed against each other, and, together with the fold *p*, which is likewise pressed down, effectively protect the urino-genital

apparatus. This explains why in the Tortoises defæcation and micturition are separate acts. How the penis becomes doubled up is not very easily seen; probably through the greater elasticity of its grooved side and through the contraction of the walls of the cloacal chamber.

The vestibulum cloacæ is capable of considerable shortening through the longitudinal unstriped muscles of its walls and through the paired M. pubi-caudalis, which —arising from the transverse processes of some of the caudal vertebræ near the anal opening, and being attached to the splanchnic side of the pubic symphysis—can by its contraction bend the tail; at the same time both muscle-bands exert a pressure upon the lateri-ventral walls of the outer cloacal chamber. Anal muscles proper, like a distinct sphincter, are not developed in the Chelonia. The M. ischiocaudalis (flexor caudæ ischiadicus of Bojanus) arises from most of the postsacral and caudal vertebræ; its fibres run transversely, and form a broad, although thin, muscular layer, which, besides on the tuber ischii, is inserted aponeurotically on the visceral side of the ischiadic symphysis. From the caudal corner of this symphysis to the anus the muscle-fibres meet with those of the other side, and being partly attached to the cutaneous lips of the anus, bridge over the whole cloaca. They act upon the latter as a constrictor. Some of the most superficial fibres, between the caudal margin of the ischium and the anterior corner of the anus, assume a more longitudinal direction and an independent aspect; they are described by Bojanus as dilatator cloacæ, whilst in Testudo græca they are hardly developed.

In the *Birds* (fig. 15) a typical M. sphincter ani is formed from the same muscular layer just described in the Chelonia. This layer is differentiated into two muscles: (1) M. transverso-analis; it arises in a variable way from the distal caudal portions of the pelvic bones: in rare cases also from the transverse processes of some caudal vertebræ; its fibres form in the medio-ventral line a more or less aponeurotic junction with those from the other side, and are also attached to the anterior margin of the anal opening, where they are blended with (2) the M. sphincter. The fibres of the latter surround the anal opening in the typical way, and have no connexion with skeletal parts, except indirectly where there are a few muscular slips attached to the flexor muscles of the tail or to the skin in which the tail feathers are lodged. The M. sphincter and the M. transverso-analis are, like the Cloaca, supplied by nerves from the plexus pudendus. In *Rhea* (fig. 15) there is on each side a double M. levator ani, which arises from the distal portions of the pelvic bones, and is attached to the dorsal corner of the anus. It is probably a differentiation of the M. transverso-analis. We can derive the Avian arrangement easily from that of the Chelonia if we imagine that in the Birds the M. ischio-caudalis of the Chelonia has lost its origin from the tail, and that a separation took place between the anal portion (future M. sphincter) and the portion between the anus and the pelvic bones. The rest of the reptilian ventri-lateral muscles between tail and pelvis is represented in the Birds by the MM. pubi- and ileo-coccygei.

In those Carinatæ which, like the *Anatidæ*, possess a copulatory organ, the latter is placed slightly asymmetrically on the left side of the ventri-lateral cloacal wall. In connexion with its basal portion are several muscular bundles, which somehow seem to be able to protrude and to retract the penis. They are merely branches from the inner portion of the voluntary sphincter ani, which itself in its ventral half is more developed towards the left side. It seems probable that through the action of the inner portion of the M. sphincter the vestibular walls can be everted, and that with them the penis is protruded.

In the *Ratitæ* the strongly-developed copulatory organ necessitates the presence of special copulatory muscles. There is in *Rhea* on each side a M. protractor penis, which in a similar way as in *Anas* is developed from an inner layer of the sphincter, but it goes as a rather independent muscle to the lateral portion of the basis penis. In *Struthio* it receives a slip from the M. transverso-analis, which descends from the pelvic bones. A pair of retractores penis arises from the pelvis, and is attached to the ventral aspect of the middle portion of the organ.

The copulatory muscles of the Carinatæ are consequently derived from the M. sphincter ani solely, whilst in the Ratitæ they are partly also differentiations of muscles, which are still attached to the pelvis, and are therefore skeleto-genital.

Saurii.—The numerous anal and copulatory muscles of the Lacertilia have been described and figured in the 'Morphologisches Jahrbuch,' vol. 7. The striped retractor muscles of the two penes cannot be compared to any of the other Sauropida, although they are likewise differentiations either of the ventral caudal muscles or of the M. sphincter. The latter is almost independent, arising, however, from some of the first transverse processes of the tail vertebræ. *Hatteria* possesses a M. perinei *s.* transverso-analis like the Lizards; also a M. transversus medianus almost exactly like that described in the Crocodilia; its most superficial fibres are transformed into a distinct outermost sphincter, which, according to the shape of the anal opening, lies transversely and not longitudinally as in the Crocodilia.

From the outside of the M. transversus medianus, and covered by the M. sphincter, starts on each side a broad but thin muscle, which runs back and attaches itself aponeurotically on the skin and on the fascia of the ischio-caudalis, behind the anus. It resembles a very similar pair of muscles of the Lizards.

The odoriferous glands receive a coating of striped muscular fibres from the M. transversus medianus.

The anal and copulatory muscles of the *Mammalia* show the greatest differentiation.

In the *Monotremata* a broad, striated muscle arises from the ischium and attaches itself with a small portion to the root of the crura penis, sending at the same time fibres along the dorsum of that organ; it is a M. ischio-cavernosus; its greater portion, however, runs along the ventral and lateral walls of the cloaca, attaches itself to them, and extends as far as the sphincter ani, with which its fibres partly blend. Through the action of this muscle undoubtedly the cloaca can be considerably

shortened, and, since the penis is not attached directly (except through the ischio-cavernosus) to the pelvis, the organ can be protruded. The sphincter cloacæ externus is strong, and an inner portion of it shows the division into a sphincter ani and a sphincter of the opening for the penis. Retraction of the copulatory organ is perfected (besides by the relaxation of the M. ischio-cloacalis just described, and by contraction of the pelvic portion of the ischio-cavernosus) by the assistance of a small non-striped muscle, running along the dorsum to the glans penis, and forming the continuation of the longitudinal muscular layer of the sinus uro-genitalis. During the erection this small muscle acts as *M. levator penis*, with which it is homologous in other Mammalia.

The sphincter ani consequently does not take a share in the muscle-supply of the copulatory organ, and thus exhibits a difference from the Birds and Lizards.

All other Marsupial and Placental Mammalia possess likewise a muscle which arises from the pubischium and which grasps the crura penis; it may, however, arise from the ischium or from the pubis only (M. ischio-cavernosus *s.* erector penis).

The sphincter ani externus and the M. bulbo-cavernosus are to be looked upon as originally one mass, divided, hand-in-hand with the disappearance of the cloaca, into a dorsal portion or anal sphincter, and into a ventral portion or M. bulbo-cavernosus, *s.* accelerator urinæ (constrictor vestibuli in the female), with a third portion, the M. urethralis. The M. levator ani, the M. transversus perinei, and the M. ischio-cavernosus remind us of the Ratite arrangement. A M. levator penis is found in most Mammals, and is fixed to the dorsum penis. Sometimes, *e.g.*, in Chiromys and in the Marsupials, it arises from the crura penis or from their fascia, and, therefore, still retains Monotreme conditions. In most Placentalia it has become attached to the skeleton, arising from the symphysis pubis (Rodents, Elephants) or from the fascia below it (Monkeys), from the ischial tuberosity (Hedge-hog), from the pubis and ischium with a broad origin (Horse), or, lastly, from the first caudal vertebræ, in which case it passes to the right and left from the rectum (Carnivora). In Man it is much reduced. Its chief action is frequently only the compression of the venæ dorsales penis.

Attached to the urethral side of the penis, sometimes extending down to its glans, is another, often very powerful, likewise non-striped muscle, the *retractor penis*, fig. 28. It is best developed in those Mammals in which the copulatory organ is lodged in a canal formed by the abdominal skin, but it is absent in the Rodents and Carnivora, and in those Mammals which have a free or pendent copulatory organ (Primates, Chiroptera).

It arises either from the sacrum or coccyx (Marsupials, Horse, Boar), and passes in this case on each side of the anus, or it comes from the ventral region of the sphincter ani (Cetacea, Ruminants); in the Bull it attains a length of about 30 cms., and each of its halves is more than 1 cm. in thickness.

Distinctly copulatory muscles in the Mammalia are consequently derived from

skeletal and also from non-striped muscles. How such involuntary muscles can be separated off from the longitudinal muscularis of the intestinal canal is shown, besides by the M. levator of Ornithorhynchus, by the Crocodilia. There is in Alligator (figs. 3–5) a broad, rather double band of non-striped muscle, which, near the place where the ureters enter into the cloacal wall, leaves the latter, perforates the voluntary M. transversus cloacæ, and firmly attaches itself to the fascia which covers the M. ischio-caudalis, rather near the medio-ventral line. There can be little doubt that this muscle is an additional protractor or shortener of the cloacal chamber, and helps to bring the copulatory organ to the surface.

II. *The Nerve-Supply of the Cloacal Region.*

The lumbar and sacral plexus of the Reptiles has been described and figured in the 'Morphologisches Jahrbuch,' vol. 7, but without reference to the plexus pudendus proper.

In *Alligator mississipiensis* (fig. 3) the primary sacral nerve S is as a rule the twenty-sixth spinal. The obturator nerve is composed of $\frac{a+b}{x}$, whilst the ischiadic plexus is formed by the greater portion of a, the entire stem S, and a considerable part of α, which is the first postsacral nerve. α sends out the following branches:—1. Several strong branches to the powerful M. caudi-femoralis, which receives further on a similar supply from β and γ. 2. A long nerve which passes to (*cf.* p. 10) the caudal margin of the symphysis ischium, and then supplies a portion of the M. rectus lateralis, the M. transversus lateralis *s.* medianus, *i.e.*, the striped muscles of the anus. 3. Several entirely cutaneous branches are distributed over that region.

β and γ supply, like the other caudal spinal nerves, the M. caudi-ischiadicus; the share of β in this is, however, very small.

The stem β receives a branch from γ and from α, through which combination a sort of individually most variable plexus is formed; it supplies with several branches the muscles of the dorsal and of the lateral wall of the urinary chamber, and, moreover, the penis or clitoris, and lastly through many ramifications the rest of the whole cloacal vestibulum *s.* proctodæum.

The sympathetic system is arranged as follows:—In the lumbo-sacral region down to α it is very regularly composed of metameric ganglia, rami communicantes, &c.; the peripheral branches supply the testes, kidneys, blood-vessels and the gut; no changes regarding the nervous system are visible at the level of e, the fifth presacral nerve, at about which level the ileum passes into the rectum.

A remarkable change, however, takes place at α. The usual ganglion is somewhat removed from the stem on to the lateral chain, and numerous nerve branches are sent to the intestinal wall. In level of β all this is changed. The sympathetic system is reduced to a paired chain, composed of very thin rami communicantes sent from β, γ, δ, &c. There are no ganglia visible, and the chain supplies merely the caudal

vessels. No branches are sent to the cloaca, the anus, or to the copulatory organ. This break between an essentially vasomotor and an ordinary visceral supply taking place between α and β coincides fairly well with the end of the rectum and the beginning of the interior cloacal chamber *s.* urodæum.

Microscopic examination of osmic preparations of the various nerves mentioned above showed the following:—

Nerves supplying the M. caudi-ischiadicus.—The ordinary somatic structure.

Nerves of stem β, supplying the rectal wall.—Consisting of two portions, one non-medullated, the other with fine medullated fibres.

Nerves to the penis.—Many non-medullated ("sympathetic" vaso-motor), and many fine medullated (visceral) fibres; the whole nerve agreeing exactly with a typical N. erigens in structure.

A piece of nerve of the lateral sympathetic chain between γ and δ agrees much with the rectal branches from β; it is a visceral nerve with small medullated fibres, and a large amount of non-medullated fibres.

In the Lizards the anal and sexual muscles are likewise supplied by postsacral nerves, which chiefly belong—like in the Crocodiles—to stem α in *Monitor, Cnemidophorus, Hatteria;* or to stems $\alpha+S$ in *Cyclodus, Platydactylus, Lacerta viridis, Ophryoessa, Polychrus;* or to stems $\alpha+\beta$ in *Chamæleon.*

The cloacal region in *Emys* is supplied chiefly by the 22nd+23rd+24th nerves, *i.e.*, $\gamma+\delta+\epsilon$, the penis by the 24th and 25th$=\epsilon+\zeta$. The same formula applies to *Testudo græca.* All these cloacal and copulatory nerve-branches run between the cloacal lateral walls and the M. lumbo-caudalis and M. pubi-caudalis, branching off from the whole spinal nerve-stems near the middle line.

III. *The Modifications of the Cloaca.*

The internal or cephalic end of the cloaca of the *Crocodilia* is marked by a very prominent ring-wall (fig. 23, *rc*), which is produced by the concentration of the circular muscular fibres. Somewhat half-way between the cephalic end and the anal opening is another fold (fig. 22, F), chiefly formed by the submucosa of the cloacal walls, most prominent on the dorsal side. These two semi-lunar folds are frequently so high and well developed that their opposite lips touch each other. They divide the whole cloaca into two chambers. The anterior, inner or cephalic, one has the same coatings as the rectum, but its inner walls are smooth and different in structure from the rectum. Into the dorso-lateral sides the ureters open separately, just above a prominent papilla. This chamber is either empty, or filled with the clear, almost colourless urine, which can distend this "urinary chamber" into an oval shape of very large size. It never contains fæces, which only pass through it. Such a chamber is peculiar to the Crocodilia. At the first glance we should compare it either to the chamber UD, or, because of its shape and partial function, to the chamber CD of

Saurians and Birds, but in neither case would the folds bordering its cephalic and caudal ends correspond with those of the other Sauropida. In fact the urinary compartment described above is homologous with the chambers UD and CD of the Saurians, Snakes, and Birds. This I am able to prove by the condition of things prevailing in very young, but already hatched, Crocodilia (fig. 23). In *Alligator mississipiensis* (snout to anus 13 cms.) the ureters open into a small roundish chamber, which is bordered head- and tailwards by a high and very prominent circular fold. The fold towards the head is situated closely above the urinary orifices, and leads into a slightly larger chamber, CD, the inner walls of which are very irregular through high longitudinal and oblique folds; the lumen of this chamber CD is small, and shows the same internal structure as the rectum above, from which it is separated by another prominent and very thick fold. Externally both chambers CD and UD are surrounded by a powerful layer of chiefly circular muscles, which mark the termination of the rectum very distinctly, and give the chambers UD and CD the external appearance of one swollen bulb. The inside of both chambers shows numerous folds, finer and more villous in UD. In young *Crocodilus palustris* (snout to anus 11 cms.) a very similar condition prevailed, but the inside of chamber UD was smooth, velvet-like, and remarkably different from that of CD, the mucosa of which showed the same structure as the upper rectum. In young *Crocodilus biporcatus* (snout to anus 15 cms.) a remarkable difference is observed. The fold *rc* has almost entirely disappeared, and the chamber CD, besides now forming one compartment with UD, is considerably elongated; the inside shows only a few longitudinal folds, the walls of the two united chambers are thin, and much of the former strong muscular coating has given way to thin longitudinal fibres.

In still older specimens of Crocodilus and Alligator the original two chambers are transformed into one thin-walled, much-distended, and inside almost smooth compartment, shut off from the rest of the rectum by a sphincter and fold like that of the adult. This shows that the peculiar arrangement of the adult Crocodilia is secondarily acquired, and that part of the rectum, viz., CD, is transformed together with UD into a room intended for the exclusive retention of urine. The outer, posterior or extra-pelvic chamber (vestibulum) is characterised by a much stronger development of the longitudinal muscles, a considerable portion of which goes as a detached band to the post-anal region of the tail (*cf.* p. 14); its dorsal wall is much longer than the ventral, like in all animals with a longitudinal anal opening. Near its lateral margin opens on each side a complicated musk-gland at the fundus of a deep recessus. The walls of the latter can, like those of the gular musk-glands, be everted at will like the finger of a glove, chiefly through the pressure of the superimposed M. sphincter transversus. The smeary contents of the gland-bags are pressed out by the non-striped muscular coating of the bags, from which runs a likewise non-striped cord to the crura penis. It is generally supposed that through these strong scent-glands the sexes are enabled to find each other, but besides this sexual advantage they seem to be used as warning

organs, an idea which is suggested by the fact that all these glands secrete already in very young specimens, and that the vicious little Crocodiles (from one to two feet in length) kept in my reptile-house evert them when very angry. On the ventral wall, and immediately towards the outer side of the fold between the inner and outer chamber, is situated the penis. Its epithelial coating is continuous with that of the fold. The organ itself is attached to the caudal corner of the ischiadic symphysis by a strong and roundish fibrous band (figs. 1 and 8), which arises single from the ventral sides and forms partly the continuation of the two fibrous halves of the penis; the bulk of the crura penis (comparable to the corpora cavernosa) is not attached to the pelvis, as generally stated, but projects backwards towards and into the pelvis.

This portion of the crura penis is decidedly rich in lacunæ and other venous cavernosities, and is in all probability able to be swelled.

In the corner between the pelvis and the lateral side of each crus is a recessus, lined by the peritoneum. The fundus of this recessus is open and leads through a canal into the cloaca. The outer orifice of these peritoneal canals is protected by a small papilla. In the neighbourhood of these papillæ are several small blind sacs or lacunæ (*cf.* fig. 1), and further towards the glans I observed in the adult specimen of *Crocodilus niloticus* three or four soft papilla-like projections of the outer coating of this organ. They are furnished with sensory hedonic corpuscles.

The deep groove on the dorsal side of the penis ends towards the crura in a blind sac, into the further corner of which open the vasa deferentia.

In young female specimens, up to a total length of 3–4 feet, the clitoris is nearly of the same size as the male organ, but in larger specimens it is considerably smaller (*cf.* fig. 2). The whole structure of the organ is the same in both sexes, with the exception of the position of the openings of the vasa deferentia and the oviducts. The latter do not open into the recessus of the dorsal groove but on the brim, or rather outside, the intracloacal fold, close to the dorsal base of the clitoris. In both sexes, therefore, the genital tubes, although at first running along and piercing through (in the male) the dorsal cloacal wall, open in a decidedly ventral position and thus represent an arrangement similar to that of the Chelonia and Mammalia, whilst in the Lizards, Snakes, and Birds these tubes retain their original dorsal position. Moreover the whole cloaca of the adult Crocodilia is divided into a genital or copulatory and into a strictly urinal chamber, the latter being situated between the former and the rectum. As this also is an arrangement not found in other Vertebrata, it will perhaps not be unnecessary to make some remarks on the cloacal region of the other Sauropida and the Mammalia, especially because, in spite of BUDGE's first-rate monograph, we shall observe certain anatomical and physiological points which hitherto have escaped notice.

The *Lizards* represent a peculiar type (figs. 17 and 18). The transverse anal opening leads into a not very capacious cloaca, which in Lacerta is divided into an outer or more ventral and into an internal or more dorsal chamber. This division is formed

by two very large triangular flaps, one on each side, which arise from the inner, or median, root of each penis, and extend towards the medio-ventral line to the ventral or anterior margin of the anus. Each flap, more or less horizontally, lies inside the anal sphincter, so that, if the latter is closed, it is hidden from view. In the vertibulum thus formed open the penes and the neighbouring anal glands.

The slit between the free margins of the two flaps leads into a somewhat larger chamber, which is shut off from the rectum by a strong more or less circular fold. This fold is, however, very low on the ventral, but very high and thick on the dorsal wall. Thus is formed a rather deep dorsal recessus, into which open the urino-genital canals. In *Monitor*, *Lacerta*, *Anguis*, *Calotes*, the ureter and the vas deferens of each side are united into one short canal, which opens on a small papilla ; in the female the two oviducts and the two ureters have four separate openings. In the genus *Lophura* both ureters unite, form a small pseudo-bladderlike dilatation, and open on *one* papilla in the dorso-median line ; the oviducts have likewise one outer opening only, situated a little nearer towards the pelvis than the urinary opening, but they are divided by a longitudinal septum, which extends almost to their orifice.

The urino-genital recessus is surrounded by a thick and low nearly circular fold, formed entirely by the dorsal wall ; it can close the recessus almost completely. This fold is arranged in such a way that, when pressed upon by the fæces coming from the rectum, the recessus is completely protected, but otherwise it leads the urine towards the urinary bladder, or, if that organ be not developed, into the rectal chamber.

This rectal chamber is very capacious and is marked off both against the rest of the rectum and against the cloaca by high and strong semicircular folds. Its internal structure in *L. ocellata* and *L. viridis* agrees with that of the rest of the rectum (which can sometimes form another pouch-like dilatation), but in *Monitor* its quite smooth and thin walls, with a very feebly-developed layer of circular muscle-fibres, bear more resemblance to the cloaca than to the rectum.

Most Lizards, with the exception of the *Monitors*, *Amphisbænidæ*, and some *Agamidæ*, possess a true urinary bladder ; it is often of considerable size, and opens by a narrow tube on the ventral side exactly on (or slightly analwards from) the fold between the lower rectal and the urino-genital chamber. This position explains how, if the anal opening be firmly closed and the whole vestibulum be compressed, the urine can enter this bladder ; and, secondly, how, by contraction of the bladder, part of the urine can enter the rectal chamber and there mix with the fæces, which, as is well known, almost invariably contain portions of the whitish-yellow urea. This rectal pouch is, therefore, a true cloaca in the physiological sense.

In the *Monitors* the inner divisions between the vestibulum and the urino-genital chamber are not well marked, and it is only by artificial means that folds corresponding to those of the *Lacertæ* can be traced.

The *Ophidian* type (fig. 19) is similar to that of the Saurians. The rectum forms a capacious, thin-walled, and smooth chamber, which can be shut against the rest of

the rectum by a thin but high circular fold, and against the cloaca by a high and thick semi-lunar fold coming down from the dorsal wall. The cloaca forms a dorsal recessus, into which open the oviducts; this sometimes common ostium is provided with a strong sphincter, which is in connexion with the fold just described. The ureters open side by side in one common slight niche on the dorsal side, towards the caudal margin of the anus; the small lips of the niche can close this little chamber. In the male snakes the ureters and vasa deferentia of each side are commonly united. A peculiarity of the *Ophidia* is, therefore, the separate and independent position of the oviductal orifices. The whole cloaca is, although imperfectly only, divided by horizontal or oblique dorso-lateral folds into a dorso-internal or urino-genital and a ventri-external or fæcal chamber—an arrangement similar to that of the Lizards. The latter chamber represents, of course, the vestibulum; it receives in its posterior dorsal wall the penes, and on the lateral side of them the well-developed anal glands. In the female the representatives of the penes are frequently very small, and reduced to mere shallow invaginations of the postanal wall, but the anal glands are developed much stronger than in the male, and fill up the whole space otherwise occupied by the male organ. Like in the Lizards, only still more completely, the rectal chamber retains both fæces and urine, acting therefore as a cloaca.

The cloacal arrangement of *Hatteria* (figs. 12 and 13) represents a type by itself, which, however, bears resemblance to that of the Lizards.

The transverse anal slit is bordered by non-prominent lips, and leads into a rather deep triangular chamber, which is lined by the continuation of the invaginated outer skin. In this chamber are seen three deep holes, viz., in each of the outer corners the openings of the anal glands, which have been accurately described by Dr. Günther. They are of double the size of a common pea, and in the living animal have a strong, rather agreeable smell of musk and violets; the middle hole is round, and can be completely closed through the contraction of the M. transversus medianus. Its walls seem to possess thick lips; when cut open there is, however, only a very thin, although high, fold, which passes gradually into the lining of the cloaca, and contains no muscles. This fold is not clearly represented in any other reptile, although indications of it exist in many Lizards. The total absence of copulatory organs in Hatteria suggests that during copulation this circular fold can be protruded by inward pressure of the cloaca in order to secure conception. It would then bear a striking resemblance to the arrangement found in the Cœcilia (*cf.* p. 27). This hole leads into another chamber which in a half-grown female was 7 mms. long; its walls are lined with mucous membrane thrown into slight longitudinal folds. Inwards, towards the pelvic end, this chamber is bordered by another fold; this is circular, thick at its base, thinner at its free margin, and towards the dorso-median line it is raised into a triangular or conical flap, which is about 5 mms. high, and fits into the opening of the bladder in the opposite ventral wall. This fold corresponds to the fold F of other Reptiles. The next chamber is wider and longer and of the same

structure as the previous one, but with softer walls. Into it opens in the medio ventral line the long-necked bladder, and near the dorso-median line open on each side, near the base of a papilla, the ureters and the genital ducts. In the female there is one opening only for the oviduct and for the ureter of each side. This urodæum, or urino-genital chamber, is as usual shut off from the rectum by a high circular fold. Peritoneal canals are indicated by two recessus of the body cavity, which laterally, from the urino-genital orifices, extend into the cloacal wall, and below the fold F end each in a small non-perforated papilla. The latter were best developed in the male, and are represented in fig. 12.

The *Avian* type (figs. 14, 15, 16, 20, 21) is an interesting modification of both the crocodilian and the saurian arrangement. The determination of the various chambers is beset with difficulties because of the extreme variability of the separating folds.

The whole cloaca of most birds is divisible into a vestibulum, a urino-genital or middle chamber, and a rectal or innermost chamber.

The middle or urino-genital chamber is small ; it receives in its dorso-lateral walls the ureters and the genital ducts, which are frequently protected by papillæ. Immediately above (headwards from) the uretro-genital orifices is a circular fold *rc*, most prominent on the ventral side ; below the orifices, *i.e.*, towards the tail, is always present a well-marked fold F (*sphincter vésical* of Martin-St.-Ange), best developed on the dorsal and lateral sides, whilst towards the ventral aspect it goes over into the coating of the copulatory organ, when such is present ; sometimes, however, the fold is nearly circular, and very distinct. The room between this fold and the outer anal opening is homologous with the vestibulum of other Amniota ; it lodges the copulatory organ ; a wide opening in its dorsal wall leads into the bursa Fabricii. The entrance to this pouch is sometimes, *e.g.*, Struthio and Leptoptilus, guarded by a valvular fold, and divides the whole of the vestibulum, according to Geoffroy, into a *bourse du prépuce* and a *bourse accessoire* (bursa Fabricii) ; this fold is, however, unimportant, and absent in many birds. That the bursa often forms a mere dorsal dilatation of the vestibulum has been shown and explained by Forbes. Near the sides of the penis, in various positions, are often found in both sexes glandular pores (Cowper's glands, Geoffroy), reminding us of similar pits in the Crocodile. They occur, however, also in birds which possess no copulatory organ, and seem, therefore, to belong to the vestibulum itself; their analogy with anal glands of other vertebrata seems remote. The third chamber is situated above the urino-genital one, and this presents some difficulties. In most birds it forms an oval dilatation of the rectum, and is of considerable size. In Casuarius and Rhea it goes gradually over into the rest of the rectum, and its inner walls agree in structure with the latter, but in many Carinatæ, and in Struthio, the cephalic end of this chamber is marked by a very well developed circular fold and sphincter-like constriction, and, in connexion with this, the inner structure of the walls is smooth and very different from that of the rectum. Transitional stages are, however, numerous. Moreover, in Struthio this chamber is

followed by another smaller and less defined one. The succession of the chambers in Struthio therefore resembles much that of certain Saurians and that of very young Crocodiles.

It follows, from the arrangement described above, that in birds the urine is not retained in the small urino-genital chamber, but that, like in lizards and snakes, it passes into the next compartment above. Through this pass, of course, in all birds the fæces; if the latter are very loose and watery, like in the raptorial birds, ducks, herons, cormorants, they collect in the then very capacious room, together with the urine, and transform it into a cloaca. If the fæces are more resistent, *e.g.*, in geese, they are generally retained in the rectum, above fold *r*, and simply pass through the cloaca, unless, as in sitting birds, an unusual accumulation of excrements takes place. In the Ostriches defæcation and micturition are mostly separate acts, especially when through a large development of the bursa Fabricii a physiological (dorsally situated) bladder is produced.

The *Chelonia* (fig. 10, 11, 24, 25) represent a type somewhat intermediate between that of the Ratitæ and that of the Monotremata, at the same time bearing slight resemblances to that of the Saurii. The rectum is separated from the cloaca by a very distinct circular inner sphincter, *rc*, fig. 25. The genital ducts and the ureters open separately into a wide urino-genital sinus, which through a wide neck leads into the large ventral urinary bladder; on the other hand it stands in communication with the cloaca by a large aperture. This aperture is surrounded by a partly transverse, but chiefly longitudinal, horizontal fold, the right and left halves of which can by approaching each other completely close the urino-genital sinus, and in fact do so firmly in the living animal. The walls in the recessus recto-vesicalis project over the opening of the sinus, as shown in figs. 10, 11, 25, and 26. In the female they generally do not extend far enough towards the tail to reach the root of the clitoris, because this organ is, when very small like in Chelys, very far removed from the sinus. In the male, however, the crura penis extend so far back towards the rectum that the end of the dorsal groove of the organ can, with the help of the folds, receive the sperma. The fold *p*, namely, is continued (*cf.* p. 1, fig. 11) into the loose sheath-like covering of the penis, and gradually passes over from the margins of the longitudinal groove towards the dorsum penis, and near the glans it goes over into the thin ventral walls of the vestibular portion of the cloaca, as visible in fig. 10, near the insertion of the M. retractor penis. A result of this somewhat complicated arrangement of this cloacal-penial fold is that the copulatory organ in its proximal portion is situated rather outside the cloaca, whilst the terminal portion, or glans, is freely projecting into the cloacal lumen. Moreover, when the organ is relaxed and withdrawn, the whole cloacal-penial fold surrounds the organ like a rudimentary preputial sheath, which then bears a considerable resemblance to the conditions in Ornithorhynchus, fig. 27.

We can reduce the Chelonian cloacal type to the general Sauropidan arrangement

by the assumption that the ventral portion of the original chamber U D has been developed and partly shut off from the rest. Through the development of such a sinus urino-genitalis, the separation into a ventral or urino-genital-copulatory, and into a dorsal or fæcal portion of the "cloaca," is introduced, although imperfectly. At any rate there is no longer any retention of urine and of fæces in one common chamber: micturition and defæcation have become separate acts which exclude each other. *Cf.* also p. 11.

Paired anal pouches (cloacal bladders, anal sacs, &c.), opening by wide apertures into the dorsal wall of the cloaca opposite the urino-genital sinus, are present in the amphibiotic Emydes and in the more aquatic Chelydæ, but absent in the terrestrial Chersidæ and in the marine Cheloniidæ, which latter have their feet transformed into fins. In most Mud Tortoises (Trionychidæ) they seem likewise to be absent. Hoffmann, however, found them in a male *T. ægyptiacus*, but not in a female *T. sinensis*.

These pouches are so placed that they can be compressed by the abdominal muscles and by the retraction of the hinder extremities, indirectly also through a peculiar mechanism in connexion with the M. lumbo-caudalis. Their walls possess often a considerable layer of circular and longitudinal non-striped muscles; their inside is sometimes villous, mostly smooth, but never glandular. The orifices of these pouches can be brought into direct communication with the cloaca, to the complete exclusion of all other openings, except the external anus (Anderson).

Anderson, and Bridge follows him, considers them as the "structural equivalents" of the anal musk-glands of the Crocodilia, but he adds that he "never particularly observed that the Chelonia possessing these pouches are more characterised by a peculiar odour than the pouchless forms." They frequently yield a yellowish grumous substance, most especially abundant in those forms which have these bladders provided with villi (Platysternum). This comparison is erroneous, as already Duvernoy has pointed out; the pouches are certainly not glands, and are developed from the middle portion of the cloaca, whilst the organs of the Crocodiles are skin glands, like those on the throat.

It has been known, since Townson, that some Chelonia draw water into the cloaca per anum. He put an Emys into coloured water, and observed that, when put afterwards into clear water, it vented coloured water. He concluded from this that water was pumped into the anal pouches, and that the latter served for hydrostatic purposes. This view has been generally accepted, and is strengthened by the fact that neither the true terrestrial Tortoises nor the marine Turtles with their specialised flippers possess such additional hydrostatic organs.

It was, however, apparently never ascertained if the pouches, and not only the cloaca, were filled with water. Anderson, with his great experience of Tortoises, remarks expressly that, although he had examined, immediately after death, nearly a hundred individuals of South Asiatic Emydes, yet in no instance had the cloacal

bladders been distended with water, whereas they often yielded the grumous substance mentioned above.

To ascertain this, I put a muzzled *Emys europæa* into a large pan of water coloured with indigo-carmine in suspended form. When taken out the following day, coloured water mixed with small blue clots was freely squirted out, followed by clear urine after pressure upon the xiphiplastron. This was repeated on several days. After four days I took the Tortoise out and at once clamped the anal opening. P. M. dissection showed that no coloured fluid had entered the intestines through the mouth. No blue stuff had entered the urinary bladder, which was half full, nor had it passed into the rectum or into the oviducts. The vestibulum cloacæ and the pouches contained a little coloured fluid, and each pouch was to the greater part filled with a large piece of clotted indigo-carmine. This could not have been collected there unless the Tortoise had frequently taken in water.

Peritoneal canals exist in all Chelonia. Their abdominal openings are situated in a recess of the peritoneum close to the sides of the neck of the bladder. Anderson has done much to clear up the great diversities contained in the descriptions of these organs by various anatomists; discrepancies which are less due to faulty observation than to too hasty generalisations. Cuvier described the peritoneal canals as terminating blindly near the glans penis in the male. Isidore Geoffroy St. Hilaire and Martin believed that, as Anderson puts it, the canals divide at their extremity into two branches, one going into the cloaca, and the other tending towards the corpus cavernosum, in this way, that it opened into the cavity of the corpus cavernosum in Tortoises, whilst it terminated in a cul-de-sac in the Crocodiles. Owen adheres more or less to this view. Rathke does not mention these canals. Stannius says that in the Chelonians these peritoneal canals "are apparently, without exception, closed at their ends."

Anderson, after most carefully conducted experiments, expresses himself cautiously: "I am not prepared to go the length of saying that there is invariably a communication between the peritoneal canals and the cloaca in the males; but at the same time there can be no doubt that in the males of *Geœmyda grandis*, *Emys Hamiltoni*, and *Trionyx ocellatus* such a communication does exist. In this respect these animals conform to the course of these canals in the Crocodile. . . . All I insist on is that in the males, as in the females, experimented upon, these canals do open into the cloaca, and in this respect conform to the general type of structure distinctive of the peritoneal canals of Crocodilia, and of the so-called abdominal pores of the Cyclostomata and Ganoid Fishes."

Hoffmann, in Bronn's 'Thierreich,' the latest writer on Chelonia, leaves the whole question open, but adds that he found, like Cuvier, Stannius, Owen, Mayer, and Lataste, that the canals of Emys, Testudo, Chelys, Chelodina, terminate blindly, and open neither into the cloaca nor through the glans penis.

My own investigations show the following results:—In a large male *Testudo*

microphyes (one of the Elephantine Tortoises) each canal was continued as a round tube inside and along the walls of the groove of the penis and ended blindly in its glans; when injected, or blown up from the peritoneal end, they admitted easily my fifth finger. Side branches or openings towards the outside, through the penis, did not exist, nor was it possible to force any fluid or air into the corpora cavernosa, although the specimen was fresh. This agrees with FRITSCH's account of a male *Testudo elephantopus*, and with MAYER's males of *Testudo græca* and of *Chelone midas*.

In a large and likewise fresh female *Chelys matamata* the canals extended along and in the ventral cloacal wall to open near the glans of the very rudimentary clitoris; they admitted a crow's quill throughout their length. The preparation is now in the Cambridge Museum.

A female specimen of *Testudo græca* (Cambridge collection) likewise shows a bristle passed through the canal. In the males I found the abdominal opening very narrow, whilst the canals in the penis are wide and terminate blindly in the glans. This agrees with MAYER's male specimens, and with LATASTE's male *Testudo nemoralis*, who, however, came to the conclusion that the canals never opened externally. Regarding the females, my observations completely agree with ANDERSON's experiments made on females of Trionyx, Chitra, Batagur, Emys.

To sum up, the peritoneal canals in female Chelonians open into the vestibulum cloacæ on or near the base of the clitoris. In the males they extend, without having communication with the cavities of the corpora cavernosa, and without ramifications, through the penis, and either terminate blindly in the glans (*Testudo elephantopus*, *T. microphyes*, *T. græca*, *T. nemoralis*, *Chelone midas*), or they open into the cloaca through a small orifice "situated at the base of the glans and close to the inside of the genito-urinal groove." ANDERSON (Geœmyda, Emys, Trionyx).*

Probably all the Chelonia possessed open peritoneal canals. Considering the small size and the position of the clitoris, it is not astonishing that the canals remain more superficial and retain their openings, whilst they are completely surrounded by the much larger male organ, and that their terminal orifices sometimes become closed.

It is, we trust, not too hasty a generalisation to say now that the canals are closed in the males of the exclusively terrestrial and marine species (Chersidæ and Cheloniidæ), but that they are open in all females and in the amphibiotic and fresh-water Chelonians.

The function of these canals has always been a puzzle. That they have a function is more than probable. I observed in a female Chelys a condition similar to that mentioned by ANDERSON in other species: "The peritoneal canals have their inner walls more or less coloured near their distal ends with fine dark lines of the same

* HOFFMANN says that according to ANDERSON the canals open outwardly also in the male of *Testudo platynotus*, which of course would be a rather serious exception to the other Testudines, but ANDERSON never mentions a male *Testudo*.

pigment as that of the clitoris itself, thus indicating the continuity of the living membrane with that of the external surface. The canal was also partially filled near its end with a grumous substance, but quite different from the coagulated blood that filled the corpus cavernosum."

Duméril and Bibron suggested that the animals pumped water through these canals into the abdominal cavity, to counteract the effects of too much evaporation during the hot season. To this view Anderson assents. But this hypothesis must fall, first, because in the very species, which possibly might need such an arrangement, viz., the Land Tortoises, the male canals are closed; and, secondly, because the often extremely narrow and frequently papillary external orifice suggests that nothing can pass inwards, whilst the reverse is practicable. Moreover, to receive swamp water into the abdominal cavity would imply the greatest danger.

Geoffroy St. Hilaire and Martin gave a better explanation, viz., that any fluid, which somehow or other might collect inside the peritoneal cavity, could be drained off, and that consequently Tortoises could not suffer from dropsy unless the canals were obliterated, but this suggestion was marred by the addition that "le liquide, probablement séreux, que transmettent ces canaux, doît être porté en grande partie dans les corps caverneux, d'où il semble qu'il puisse refluer dans les veines." To this mistake they were necessarily led, because they thought there existed communication of the canals with the cavities of the corpora cavernosa.

Mayer found, I think, the right solution for those males in which the canals are closed at their extremities; the serous fluid can be pressed into the penial canals and thus assist erection. In Tortoises there is often a considerable quantity of serous fluid in the peritoneal cavity. I extracted from a perfectly healthy male *Testudo græca*, immediately after death, 10 cubic cm. of a fluid, which analysis showed to be serous, whilst perhaps the same amount of fluid remained in the animal. 20 cubic cm. is certainly a great quantity for an animal not larger than the common Land Tortoise. However, when the canals are open, like in the female, their function must, like in the Crocodiles, be a different one. In this case they can only serve as a sort of safety outlet for the fluid when the abdomen is overfilled with eggs, or if, for some unknown reason, too much of this precious fluid has been accumulated; the latter alternative applies to the male, unless we allow for the persistence of the canals by inheritance from the other sex. This suggestion, although made with great reluctance, is hitherto, nevertheless, the only one that can stand anatomical and physiological reasoning.

If we homologise the peritoneal canals with the abdominal pores of Fishes, they were first used as outlets for the sexual products, *i.e.*, they were in the service of the generative system. In the same service, although modified, they are in certain male Tortoises. In the other cases they possibly drain the body cavity, and would then, if they really are remnants of segmental tubes, have returned to their most primitive function.

The Chelonian cloacal arrangement, as described on p. 21, occurs again, with slight

modifications towards a higher type, in the *Monotremata* (*cf.* fig. 27). The differences lie chiefly in the relative size of the chambers UD and PD, and in the circumstance that the penis is lodged in a special pouch, which communicates with the rest of the vestibulum through a narrow opening close to the ventral brim of the anus. We can derive the wall PF, which separates the penis pouch from the rest of the whole vestibulum or proctodæum, from the ventral half of the fold F of the Sauropida ; the only difference is that this fold, which in Crocodiles, Birds (*cf.* figs. 14, 15, and 10), and Chelonians, gradually passes over into the loose coating of the penis, and thus forms the beginning of a preputial sheath, has in the Monotremata become considerably elongated in a longitudinal instead of a transverse direction. This I have tried to explain diagrammatically by figs. 17 to 30. Such a reduplication of the loose penial coating would almost completely separate the copulatory organ from the urodæum, and, in fact, these folds leave in the Monotremata a small opening near the root of the penis groove for the reception of the sperma from the sinus urogenitalis, but not for the urine and for the eggs. The walls of the urodæum, into which the urogenital sinus opens, are very thin, and the muscular, chiefly longitudinal, coating is likewise weak, with the exception of the voluntary striped muscle on its ventral aspect (fig. 28). This chamber UD, the urodæum, receives in the middle of its ventral wall the urine and the eggs, but not the sperma. Towards the vestibulum PD it is closed by a circular constriction and partly developed fold F, and the terminus of the rectum is marked by a strong circular muscle, which forms a powerful innermost sphincter *rc*.

Whilst in Echidna the rectum shows a large dilatation above the fold *rc*, and forms there a true rectal chamber or coprodæum for the retention of the fæces, the latter in Ornithorhynchus probably mix with the urine in the chamber UD, which in this genus is very capacious in opposition to the only slightly dilated rectum.

Bridge's remark that the existence of a complete partition between the rectum and the urino-genital opening is a characteristic point of all Mammalia, including those which possess a cloaca, is not correct, because the urino-genital sinus and the rectum are separated from each other just as much or as little in the Monotremata as in the Chelonia. Not much progress towards a higher type show the *Marsupialia* (fig. 28), and even some Rodents, Insectivores, and Lemurs. The chamber UD becomes considerably shortened, and at the same time the walls in the corner between the rectum and the sinus urogenitalis, represented in the Tortoise by the fold *p*, fig. 25, transform themselves into a growth, which, progressing more and more towards the anus, results in the almost complete division of the former cloaca into a dorsal or fæcal and into a ventral or exclusively urogenital chamber. The beginning of a perinæum is consequently derived from the fold *p*, *i.e.*, a fold inwards, above, or headwards from the opening of the urogenital sinus, and is not to be confounded with the partition PF of the Monotremata in fig. 27 ; although, of course, we have to bear in mind that the fold *p* in the Tortoises, as shown in fig. 11 at *p'*, goes over into the lateral loose coating of

the penis, which, moreover, as indicated in fig. 10, is continuous with the ventrilateral wall of the proctodæum. The preputial room of the Marsupials is therefore, strictly speaking, not completely homologous with the similar room of the Monotremes. Vulva and penis of the Marsupials, and of the Placentalia mentioned above, are still surrounded by the same external fold of skin and by the same sphincter of the anus. The shallow vestibulum is the last remnant of a cloaca.

In most *Placentalia* the cloaca is abolished by the development of a true perinæum which reaches the outer surface and secures a complete separation of the anal and urino-genital openings. The vestibulum is broken up; its dorsal portion forms the anus, whilst its ventral half, owing to the close approach of the urino-genital sinus to the surface, becomes the shallow " vestibulum " in the female, and in the male it is partly recognisable as the preputial room. The labia minora with the frenulum clitoridis are a remnant and modification of the sauropidan fold F. Lastly, in the females of these Placentalia, in which, like in Myogale, Talpa, Galeopithecus, and certain Lemurs, the clitoris is perforated by the urethra, the sinus urino-genitalis itself is divided into a dorsal or genital and a ventral or urethral half, both openings, however, retaining their intravestibular position.

A summary of the anatomical and physiological differences presented by the cloacal region of the various Amniota is given in the following table :—

Usually the cloaca is defined as a chamber at the terminal portion of the rectum, into which open the rectum, the ureters, and the genital tubes.

Balfour remarks that " in all Vertebrata the cloacal section of the alimentary tract, which receives the urino-genital ducts, is placed in communication with the exterior by means of an epiblastic invagination constituting the *proctodæum* (vestibulum cloacæ, *s.* anal chamber). The original boundary between the epiblast of the proctodæum and the hypoblast of the primitive cloaca becomes obliterated after the two have become placed in free communication. The hypoblastic section of the cloaca of birds, which receives the openings of the urino-genital ducts (our chamber U.D.), is permanently marked off by a fold from the epiblastic section or true proctodæum, with which the bursa Fabricii communicates." This fold is the one described in this essay as F. It occurs with modifications in all Sauropida, and even in the Mammalia. The fold *rc* separates the primitive cloaca from the rectum. Considering, first, that in the Crocodilia the genital tubes open decidedly into the proctodæal portion; secondly, the configuration of the Chelonian cloaca; thirdly, the occasional use as urinary receptacle of the bursa Fabricii; lastly, the condition prevailing in the Monotremes, we have to conclude that the vestibulum forms part of the cloaca.

The whole cloaca consequently consists of three successive chambers, which may be distinguished as follows :—

I. *Proctodæum* (P.D.), epiblastic = Vestibulum cloacæ, anal chamber, chambre copulatrice, bourse du prépuce, bourse de copulation, vestibule génito-excrémentitiel.

With its derivatives: 1. Bursa Fabricii.
2. Various hedonic glands.
3. The copulatory organ or organs, the at least partly epiblastic nature of which is indicated by the frequently developed horny armature of the glans.

II. *Urodæum** (U.D.), hypoblastic = Primitive cloaca, middle or urino-genital chamber, vessie urinaire, canal urétro-sexuel.

With its derivatives: 1. Urinary bladder, ventral.
2. Cloacal *s.* anal sacs of Tortoises, dorsal.

III. *Coprodæum** (C.D.), hypoblastic = Rectal or innermost cloacal chamber, poche vestibulaire du rectum, vestibule rectal.

The Urodæum is the oldest portion of the whole cloaca, then follows the Proctodæum, and lastly the Coprodæum has secondarily assumed cloacal functions.

* I propose to designate the typical urino-genital and the fæcal chambers the Urodæum and Coprodæum in accordance with Professor E. Ray Lankester's terms Stomodæum and Proctodæum; *cf.* 'Quart. Journ. Micr. Sci.,' April, 1876.

Modifications of the Cloaca of the *Amniota*.

	Coprodæum contains—	Urodæum receives—	Proctodæum.	
			Anal opening.	Copulatory organs.
Saurii, A	Fæces and urine	Urino-genital ducts; bladder present	Transverse	Double, dorso-lateral.
„ B	„ „	Urino-genital ducts; bladder absent.		
Ophidia	„ „	Urino-genital ducts; bladder absent	„	„ „
Hatteria	Fæces	Urino-genital ducts; bladder present	„	Absent.
Crocodilia, young	Fæces	Urinal ducts	Longitudinal	Single, ventral, with dorsal groove.
„ adult	Both chambers are united, receive and contain the urine only. No fæcal cloaca.		Genital ducts open into proctod.	
Aves	Fæces and urine	Urino-genital ducts	Roundish, rather square	1. Single, ventral, with dorsal groove. 2. Asymmetrical. 3. Absent.
Chelonia	Fæces only	Incomplete division.		Unpaired, dorsal bursa Fabricii.
		Sinus urogenitalis with a ventral bladder		Single, ventral, with a dorsal groove.
		And sometimes a dorsal pair of pouches.		

		Urodæum and Proctodæum.		
		Ventral.	Dorsal.	Ventral.
Monotremata		Sinus urogenitalis with bladder			Single, ventral.
„ ♀		Passes urine, fæces, and eggs		Clitoris chamber.
„ ♂		Urine and fæces		Penial chamber passes sperma.
Echidna	Dilated pouch contains fæces.			
Ornithorhynchus	No dilatation	Dilatation collecting fæces and probably urine.		
Marsupialia and certain Placentalia	Fæces only	Sinus urogenitalis with bladder. Rest of urodæum lost	Reduced to a much shortened vestibulum, with exception of a large penial chamber	Penis single, ventral, with a dorsal canal (not on the dorsum).
Placentalia	„ „	Sinus urogenitalis with bladder. Rest of urodæum lost	Dorsal portion forms part of anal opening, ventral vest., preputial room	„ „

IV. *On the presence of* Muellerian *Ducts in the Males and of* Wolffian *Ducts in the Females of young Crocodilia.* (Figs. 6 and 7.)

Rathke, in his 'Untersuchungen über die Entwickelung und den Körperbau der Krokodile,' p. 191, said that he was unable, from the embryo of *Alligator sclerops*, to ascertain if the canal running along the Wolffian body was a Muellerian duct or not. He was doubtful about the sex of his embryo.

In a male specimen of *Alligator mississipiensis*, of a total length of 25 centims., I found that the canal, which crosses the vas deferens ventrally and runs along the lateral side of the testis, was slightly rounded off at its upper end and seemed to be still open, although no bristle could be made to pass through it. This whole Muellerian duct was considerably raised above the level of the Wolffian body and duct, and was attached all along its length to a very thin and pigmentless peritoneal fold.

In another male specimen, of a total length of 33 centims., only the smallest trace of a remnant of the Muellerian duct could be made out on the upper and lower ends, whilst the middle portion had already become obliterated. This remnant of the duct was no longer prominent, but was imbedded in the same peritoneal fold as the vas deferens.

Female Alligator, total length 29 centims.—The ovary was still quite smooth on its surface ; along its lateral edge ran, closely imbedded in it, a light-coloured string, which could be distinctly followed between the ureter and the oviduct into the cloacal wall. Its upper or cephalic end projected a little beyond the anterior end of the parovarium, and was attached to a peritoneal fold like in the males. This is undoubtedly the remnant of the Wolffian duct. Laterally from the latter, fastened on to a loose peritoneal fold, ran the oviduct and opened into the cloaca a little ventrally from the Wolffian duct.

In the *Chelonia* the persistence of these ducts has been described and figured by Van Wijhe. Fig. 10 shows the remnant of the Muellerian ducts in a full-grown male specimen of *Testudo græca*. In the adult male *Hatteria* no trace could be found.

General Conclusions.

The want of an intromittent copulatory organ is in the various Vertebrata met in very different ways. The fundamental difference between the Selachian pterygopodia and any other type of copulatory organs is plainly indicated by the nerve supply, and wherever in the Amniota skeletal muscles enter into the service of copulation they have become, as shown above (*cf.* pp. 10–14), secondarily attached to the true penes long after the latter had been developed from the walls of the alimentary canal.

The first indication of an intromittent organ in the *Amphibia*, according to Wiedersheim, is a small unpaired papilla on the dorsal wall of the anal or vestibular

portion of the cloaca. It is found in Urodela only, *e.g.* in *Salamandrina perspicillata* and in *Triton platycephalus*. In the latter it consists of an erectile cone, which WIEDERSHEIM considers as derived from the caudal portion of the cloacal lips. This dorsal unpaired, median, still very rudimentary organ, is a type restricted to Amphibia.

Another type of low standing is met with in the Gymnophiona and to a less pronounced degree in Hatteria. The immissio seminis is secured by the finger-of-a-glove-like eversion of the cloacal walls, chiefly of those of the proctodæum. This type is best developed in the Gymnophiona. In them a great portion of the cloaca can through its strong muscular coating be converted into a tube projecting several centimetres, and is then used as an intromittent organ. A bifurcated M. retractor, which arises from the abdominal walls, is attached to the recessus of the middle portion of the cloaca. In the female the cloaca is short and cannot be protruded (*cf.* WIEDERSHEIM, 'Anatomie der Gymnophionen,' figs. 88 and 89, Taf. ix.).

From this stage, which probably represents that of the Proreptilia and of the true Reptiles before their separation into Crocodilia and Chelonia and into Sauria and Ophidia had taken place, we can, I think, derive the types of the other Amniota.

The definition that the copulatory organs of the Lizards and Snakes are connected with the posterior or dorsal, but those of the other Amniota with the anterior or ventral wall of the cloaca, seems to have led to the misconception that no homology can be traced between these two types of penes.

To clear this question up, I draw attention to the following considerations:—

1. In Hatteria and in the Gymnophiona, as explained above, the inner walls of the cloaca form by protrusion and evagination a temporary intromittent organ.

2. In the embryos of Lizards the anus is still round, and not a transverse slit. On each side, the lateral inner walls of the proctodæum are, together with part of the uro-anal fold F, raised up into prominent cones, which afterwards are invaginated and withdrawn into the post-anal region of the tail by the action of specialised muscles. In connexion with this the anal opening assumes its typical transverse shape.

In the Snakes, which are the most specialised branch of the Saurian stock, the original position of the penes is cœnogenetically obscured, although still traceable.

3. The original duplicity of the "unpaired" copulatory organ of the other Amniota is still indicated by the nerve supply, the vascular supply, by the corpora cavernosa *s.* crura penis, by the double penis and clitoris of certain Marsupials, like Didelphys, and by the fact that in the Chelonia the peritoneal canals are continued far into the lateral portions of the penis.

4. The completely divided right and left penes of the Lizards and Snakes are supplied by the same nerves as are the copulatory organs in all the other Sauropida.

These circumstances, considering also the modifications of the cloaca as described in this paper, seem to me to permit the following conclusions :—

That in all Amniota the intromittent organs, no matter if double or single, are derived from the walls of the outermost cloacal chamber, in connexion with the

separating uro-proctodæal fold F. The epiblastic origin of the proctodæum explains the frequent presence on the copulatory organs of epiblastic products, like horny spines, scales, sebaceous glands, and its highly sensitive nature.

That there existed a stage of phylogenetic development, during which the lateral portions of the protrusible tube became stronger, and that they specialised themselves into a right and into a left imperfect intromittent organ, the walls of which then—being stowed away in recessus of the proctodæum—escaped being used also as the walls of the efferent fæcal chamber.

That subsequently in one group, viz., in Snakes and Lizards, these penes were shifted back towards the tail and were developed into separate organs. After this had taken place they could not well meet and fuse with each other in the posterior dorsal corner of the anus, since then their bases would be too far removed from the openings of the vasa deferentia, with which they are now still connected by longitudinal folds forming the continuation of their semi-canals.

That in the other groups of Amniota the two primitive lateral erectile flaps approached each other towards the ventral side, and thus arrived at the anterior or ventral side of the cloaca. Their fusion, beginning probably at the basal part, which at the same time was further withdrawn from the surface, secured the reception of the sperma from both vasa deferentia into one canal.

That this ventral copulatory organ, now in the Reptilia restricted to the Crocodilia and Chelonia, has been inherited by the Avian stock, and has been specialised in the various ways fully and correctly described by Joh. Mueller. The struthious form comes nearest to that of the monimostylic Reptiles, whilst that of the other Ratitæ and of the Lamellirostres shows great specialisation in being evertible. The comparison of the organ, as it is found in various other Carinatæ, *e.g.*, in the Tinamoos, the Cracidæ, in Phœnicopterus, Platalea, Ciconia, shows a gradual diminution in size and a simpler structure, with all the appearance of a degraded organ. Lastly, in the majority of Birds, especially in the highest, it has disappeared, and the primitive way of everting the cloaca is again resorted to. The degeneration and final loss of such an organ, the development of which must have been caused and favoured equally by natural and by sexual selection, is a fact which we would not have arrived at by *à priori* considerations.

That the presence of a clitoris is not due to an originally hermaphroditic condition, but to direct paternal inheritance, and that it is preserved because of its hedonic nature.

That the extraordinary resemblance of the copulatory organs and the various cloacal chambers of the Monotremata to those of the Chelonia and young Crocodilia can hardly be explained by homoplastic coincidence, but that it strongly urges the phylogenetic relationship of the Mammals with the Reptiles. This, however, is only one more link in the long chain which, being anchored in the triassic Theriomorpha, in spite of Mono- and Amphicondylism, makes the Amniota more akin to each other than to the Amphibia.

Explanation of Plates.

PLATES 2–5.

Fig. 1. *Crocodilus vulgaris* (nat. size).—Ventrilateral view of the penis ; the greater portion of the outermost cloacal chamber has been cut away.

Gl. = left musk gland.
Fib. = fibrous band connecting the penis with the symphysis ischium.
Per. = continuation of the body cavity as peritoneal canal ; a probe has been passed through the left canal.

This specimen is in the Royal College of Surgeons, London.

Fig. 2. *Crocodilus* sp. ? (nat. size).—Ventral view of the cloaca and of the female genital organs ; the cloacal ventral wall has been partly cut away and the anus has been opened out, the clitoris now lying on one side. The peritoneal folds and the right oviduct are removed.

This specimen is in the Museum of Comparative Anatomy, Cambridge (No. 1377A).

Fig. 3. *Alligator mississipiensis*, ♂ (nat. size).—Left lateral view of the rectum, the cloacal muscles, and of the plexus pudendus.

B. P. = bulbus penis.
Sph. = m. sphincter.
trans. m. = m. transversus medianus.
tr. per. = m. transversus superficialis *s.* m. perinei.
pr. cl. = the unstriped muscle, described on p. 14.
v. c. = vena caudalis.
a. c. = arteria caudalis.
Sy. lat. = chain of the N. sympathicus lateralis.
S = N. sacralis = N. spinalis xxvi.
α = first presacral nerve.
α = first postsacral nerve.
cd. fm. = nerves to the m. caudi-femoralis.
v. d. = vas deferens.
u = ureter.

Fig. 4. *Alligator mississipiensis.*—The nerve branches sent from stems α and β to the penis, the anal chamber, to the lateral (R. l.) and to the dorsal wall (R. d.) of the rectum ; slightly enlarged.

Fig. 5. *Alligator mississipiensis*, ♂.—The cloacal muscles seen from the right ventral side after removal of the m. rectus lateralis.

Sy. isch. = symphysis ischium.
transv. sup. = m. transversus superficialis.
transv. med. = m. transversus medianus.
sph. = m. sphincter ani.
a = the nerve branch from stem *a* which supplies the m. rectus lateralis, the mm. transversi, and the m. sphincter.
pr. cl. = the unstriped protractor muscle.
cd. isch. = m. caudi-ischiadicus.

Fig. 6. *Alligator mississipiensis*, young ♂.—Ventral view, left side, twice nat. size, showing the left ureter, vas deferens, and the Muellerian duct.

Fig. 7. *Alligator mississipiensis*, young ♀, slightly over nat. size, showing the oviduct and the remnant of the Wolffian duct.

Fig. 8. *Crocodilus biporcatus* (nat. size).—The left half of the pelvis, together with the limb and the left half of the tail, are removed.

r = position of the fold *r*, forming the inner margin of the coprodæum.

Fig. 9. *Crocodilus acutus* (nat. size).—Ventral view after removal of the skin.

Fig. 10. *Testudo græca*, ♂ (nat. size).—The penis is stretched out, and, after removal of the pelvis, although still adhering to the cloacal walls, has been pushed over to the left side.

pb. = symphysis pubis.
pc. = visceral opening of the peritoneal canal, the course of which in the penis is dotted in.
R = rectum.
Bl. = the cut-off walls of the neck of the urinary bladder, to show its communication with the cloaca and with the longitudinal furrow of the penis. On the pigmented epididymis is seen the remnant of the Muellerian duct.
retr. p. = m. retractor penis.
pb. cd. = m. pubi-caudalis.

Fig. 11. *Testudo græca*.—Penis stretched out and laid on to the plastron to show the groove, the orifice of the uro-genital sinus, and the opening of the rectum, which is surrounded by the fold *rc*.

Fig. 12. *Hatteria punctata*, ♂ (nat. size).—The cloaca has been opened slightly to the left from the medio-dorsal line, and its walls are laid asunder. The left kidney and genital apparatus only are figured.

Bl. = urinary bladder, which was still connected with the end of the left lobe of the liver by a ligamentous stalk, the obliterated allantoic vein.

rc = fold separating the coprodæum from the urodæum; the hole in the middle is the opening of the bladder.

F = fold separating the urodæum from the proctodæum; on this fold are seen the two papillary flaps, into which are projecting the remnants of the peritoneal canals.

This preparation is in the Cambridge Museum.

Fig. 13. *Hatteria punctata*, ♀ (nat. size).—Younger specimen; ventral view, bladder and neck of bladder cut off.

F = the fold between urodæum and coprodæum, with the median dorsal flap, which fits into the opening of the bladder.

u. g. = the united left openings of the ureter and oviduct below the base of a papilla.

Gl. = the left anal gland.

This preparation is in the Cambridge Museum.

Fig. 14. *Rhea Darwini*, ♂ (reduced size).—Ventral view into the urodæum; a window has been cut into the ventral wall of the rectum.

rc = fold shutting off the rectum from the urodæum; in the latter are seen the papillæ with the uretral openings; the walls of this chamber are continued into the crura penis.

B. F. = bursa Fabricii.

This preparation is in the Cambridge Museum.

Fig. 15. *Rhea Darwini*, ♂ (the same specimen as Fig. 14, right side-view).—The right half of the rectal wall, of the urodæum, and of the proctodæum has been cut away to show the relation of the various chambers to each other and to the half-protruded penis.

sph. = m. sphincter ani.

lev. an. = m. levator ani.

R = ventral wall of rectum.

V = ventral corner of anus.

B. F. = bursa Fabricii.

Fig. 16. *Leptoptilus argala*, ♂ (nat. size, ventral view).—The greater part of the ventral walls of the cloaca has been cut away. For this drawing I am obliged to W. F. R. Weldon, M.A.

Figs. 17–29. Diagrammatic representation of the chief modifications of the cloaca, seen from the right side.—The dorso-median line looks towards the left, the ventral median line to the right side in the drawings.

CD = coprodæum = *poche vestibulaire du rectum* or *vessie urinaire* (Struthio), Geoffroy St. Hilaire; = *vestibule rectal.*

CD′ = additional rectal fæcal chamber = *vestibule rectal* of Geoffroy in Struthio.

UD = urodæum, coloured light-blue throughout the series = *vessie*

urinaire, Geoffroy; or, *canal urétro-sexuel* in Struthio; *eigentliche Kloake*, Budge; *loge uro-génital*, Retterer.

PD = proctodæum = *bourse de copulation* or *bourse du prépuce*, Geoffroy; *Vorhof der Kloake*, Budge; *vestibule génito-excrementitiel*, Duvernoy; *poche postanal+passage anal*, Retterer.

F = the fold between the urodæum and the proctodæum, shaded grey = *le véritable col de la vessie*, Geoffroy; = *repli uro-anal*, Retterer.

rc = the fold between the urodæum and the coprodæum, coloured dark-blue = *premier bourrelet ou le véritable anus*, Geoffroy; = *repli uro-rectal*, Retterer; *sphincter rectal*, Martin-St.-Ange.

rc_1 = the fold which shuts the inner end of the coprodæum, shaded with vertical lines.

sph. = m. sphincter ani, shaded with crossed lines.

p = the copulatory organ, shaded grey.

Ur. = ureter.

Gen. or v. d. = genital duct.

B. F. = bursa Fabricii = *bourse de Fabrice* or *bourse accessoire*, Geoffroy.

AS = anal pouch or anal sac.

Fig. 17. *Lacerta ocellata*, ♂.—Type A, with a urinary bladder. In figs. 17–19 one of the paired copulatory organs only is shown.

Fig. 18. *Monitor*, ♂.—Type B, without a urinary bladder.

Fig. 19. Typical snake, ♀.—*Tropidonotus.*

Fig. 20. Typical bird.

Fig. 21. *Struthio.*

Fig. 22. Crocodile, adult.—Anal glands not figured.

Fig. 23. Crocodile, very young, or embryonic.

Fig. 24. *Emys.*—Penis stretched out.

Fig. 25. *Testudo.*—Penis withdrawn.

Fig. 26. *Ornithorhynchus*, ♂, adult.

Fig. 27. *Ornithorhynchus*, ♂.—Transverse section through the middle of the urodæum.

Fig. 28. *Macropus giganteus*, ♂, adult.—Retr. = m. retractor penis.

Fig. 29. *Anthropoids*, ♀.

Fig. 30. *a–f.*—Diagrammatic representation of six stages of the phylogenetic development of the sinus uro-genitalis, and the gradual formation of a ventral chamber or uro-gonodæum.

The black line indicates the course of the sperma.

The blue line indicates the course of the urine.

a. Crocodilian stage.

b. Hypothetical stage, intermediate between Crocodiles and Tortoises. An analogous, but dorsal, recessus uro-genitalis is developed in Lizards and Snakes.

c. Chelonian stage.

d. Hypothetical stage, intermediate between *c* and *e*.

e. Monotreme stage.

f. Marsupial stage.

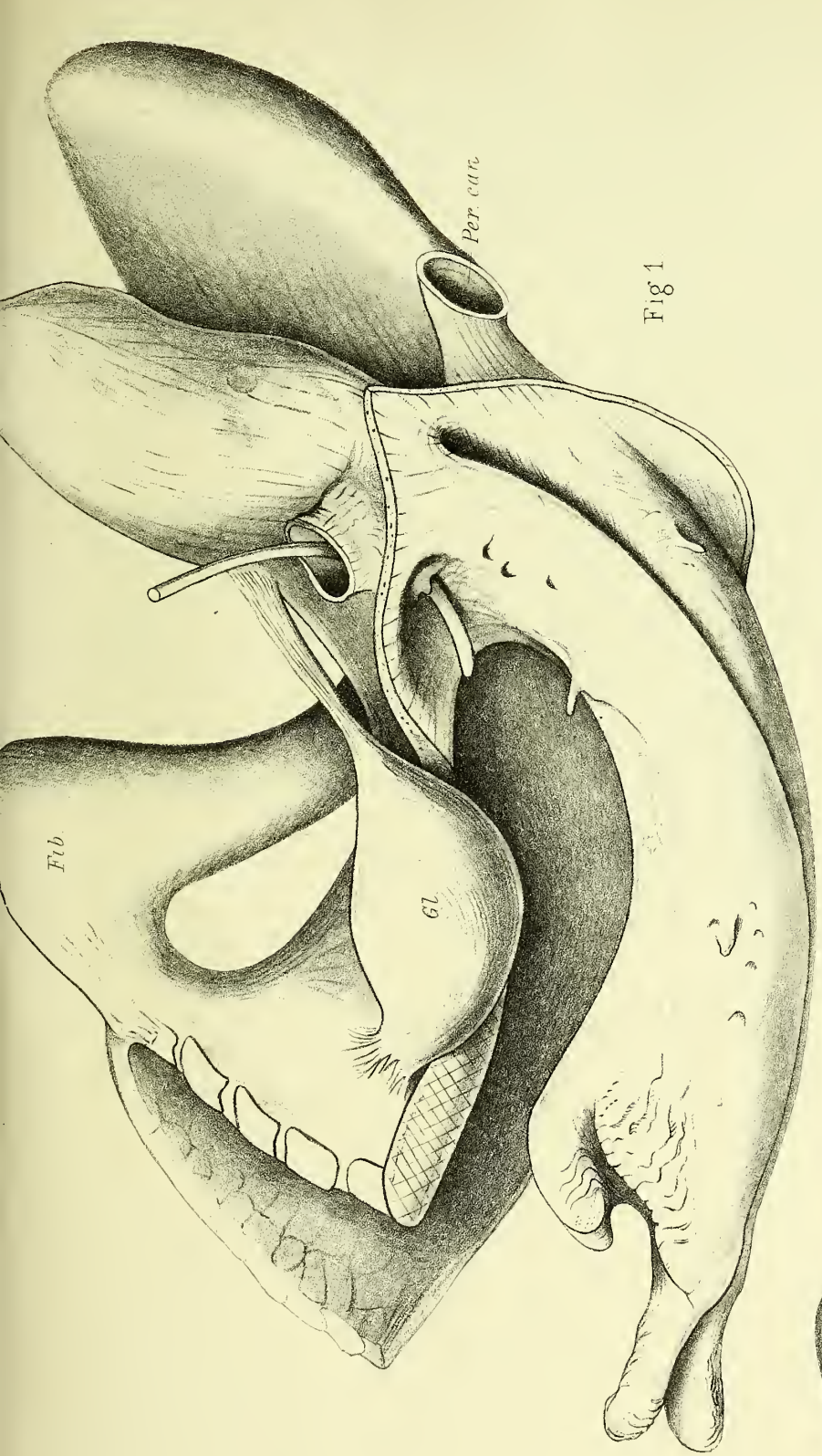

Fig 1

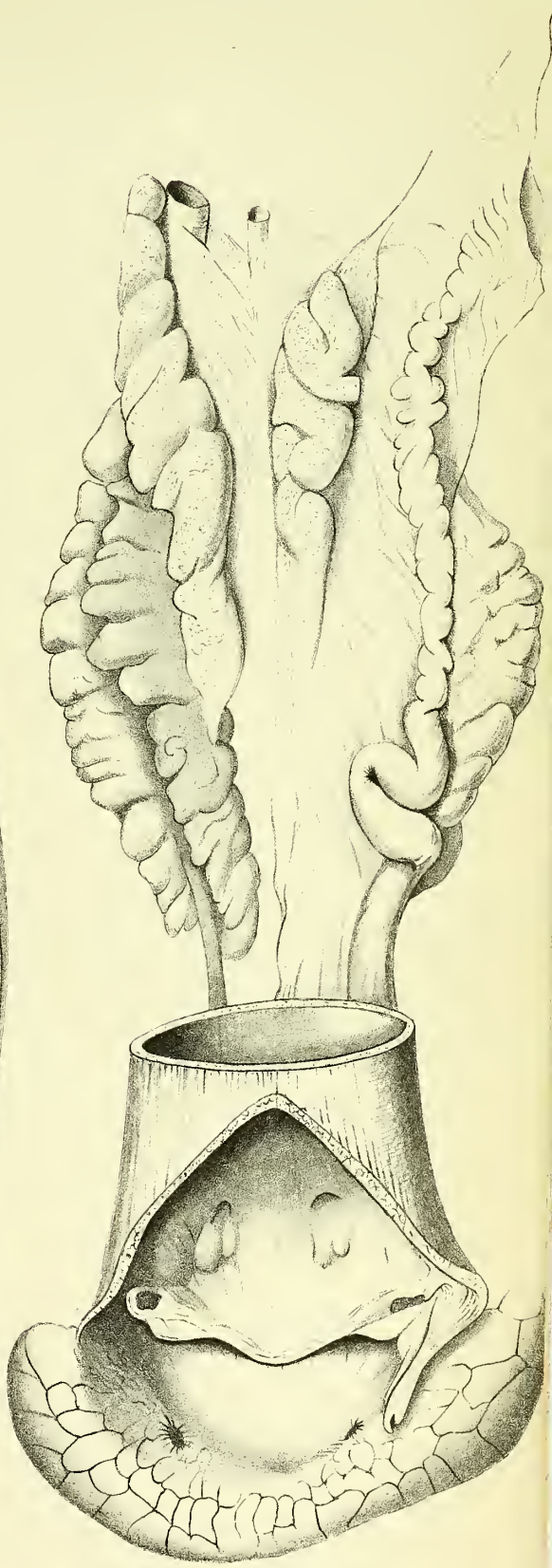

Fig 2

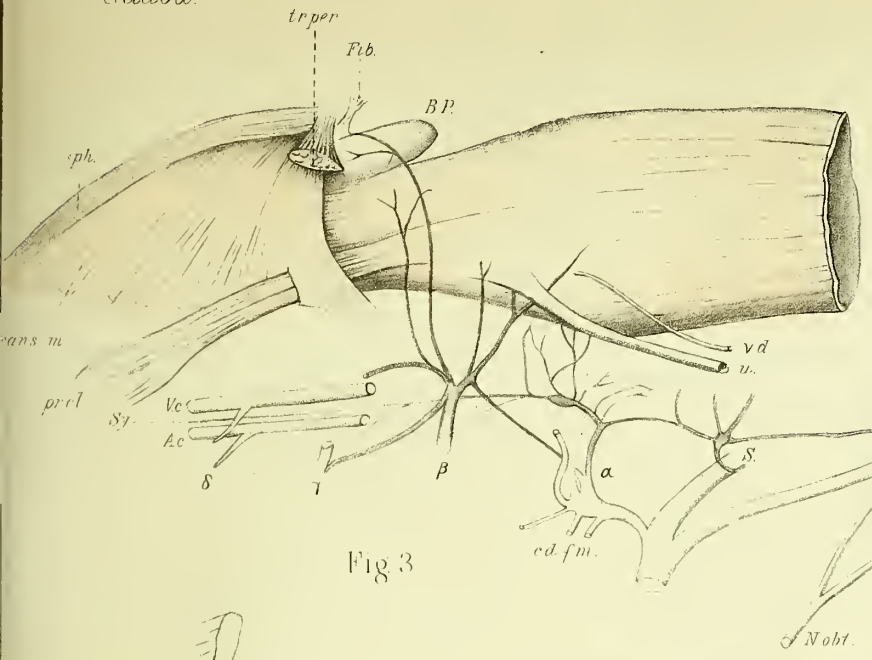

Fig 3

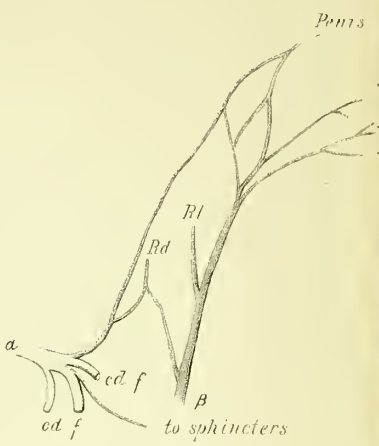

Fig 4.

Fig 5

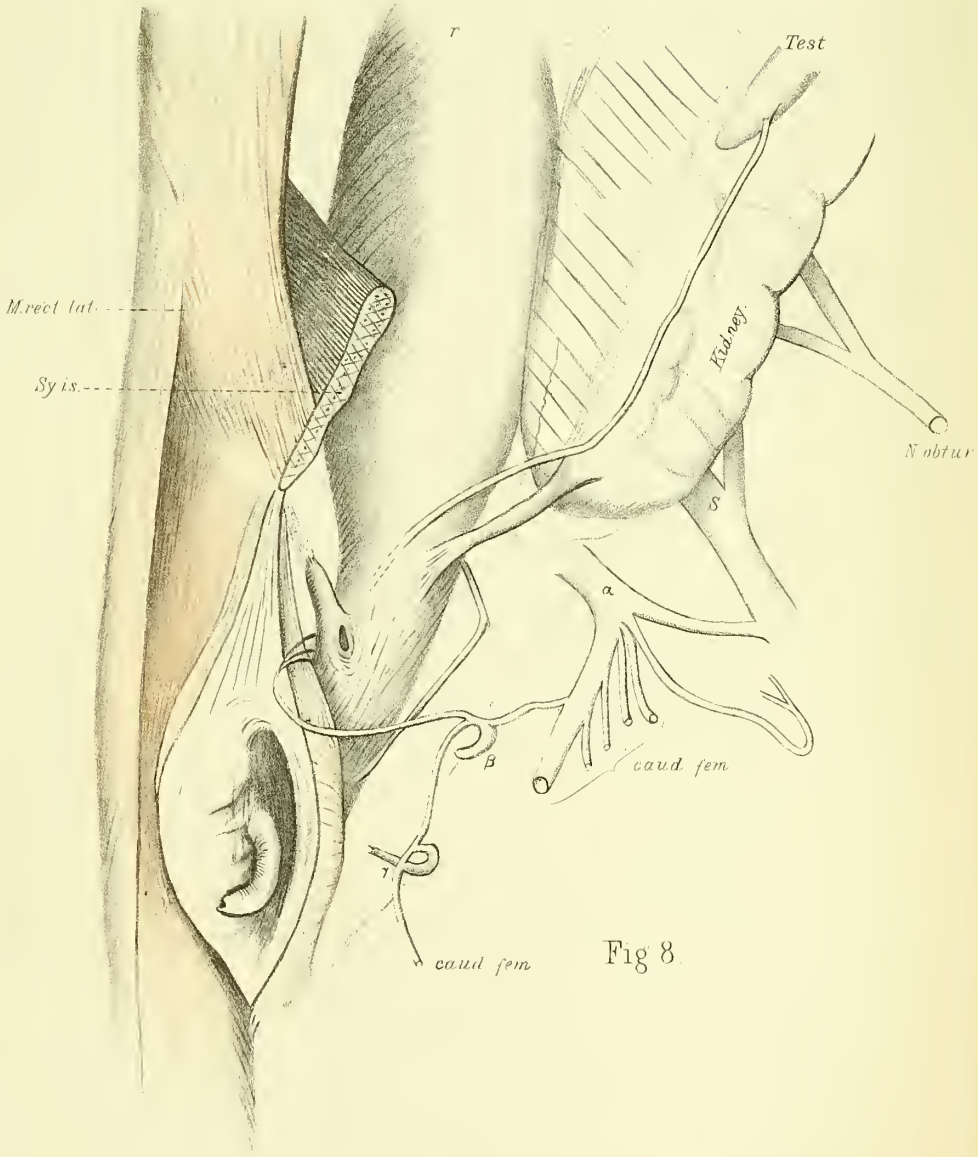

Fig 8

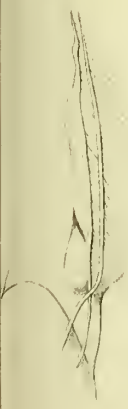

Fig 6

Fig 7


ROYAL COLLEGE OF SURGEONS OF ENGLAND
18 OCT 89
LIBRARY

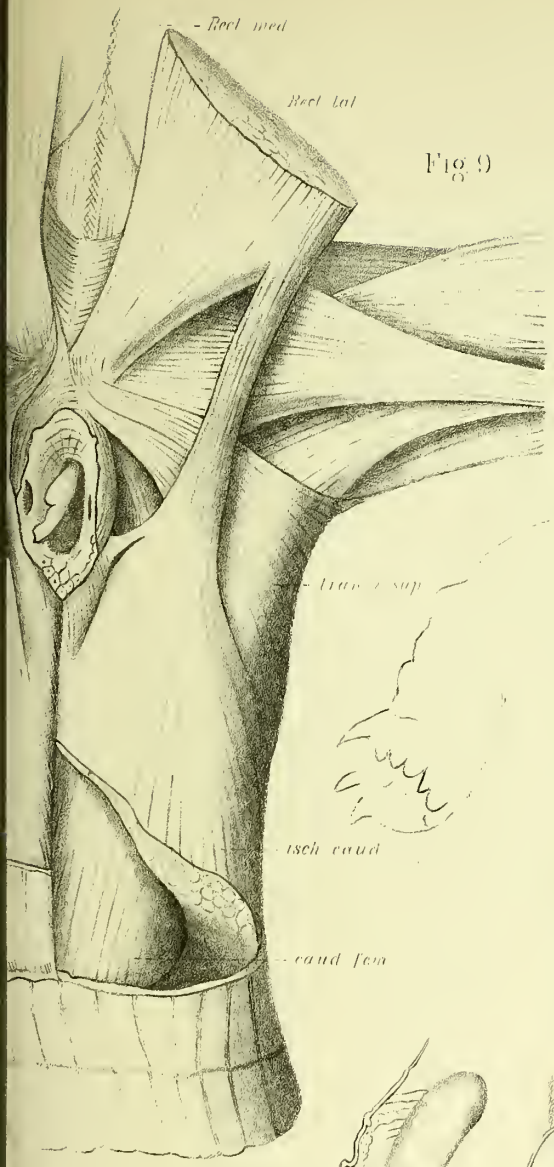

Fig 9

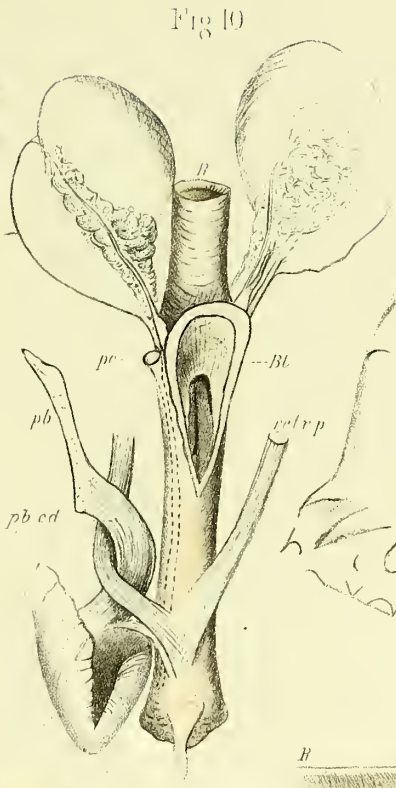

Fig 10

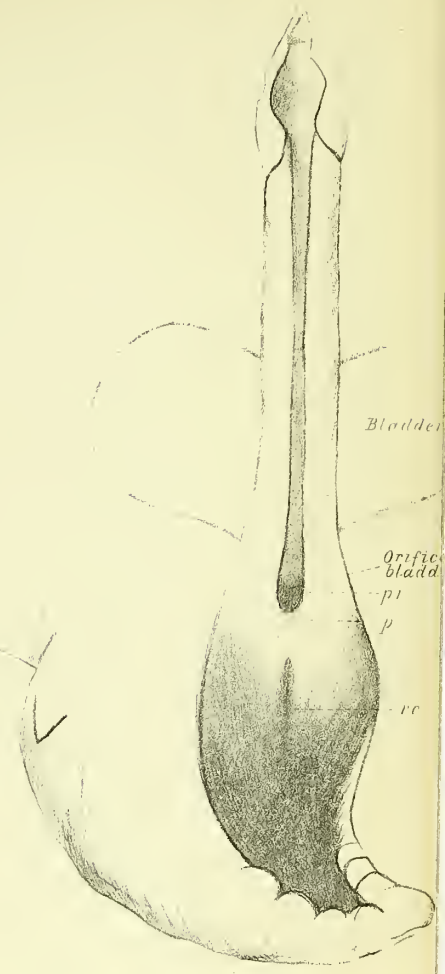

Fig 11

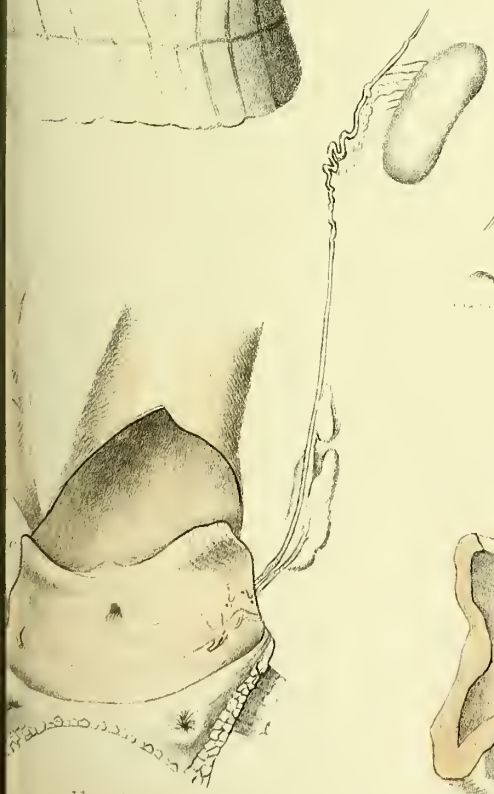

Fig 12

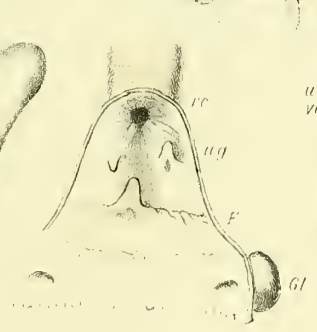

Fig 13.

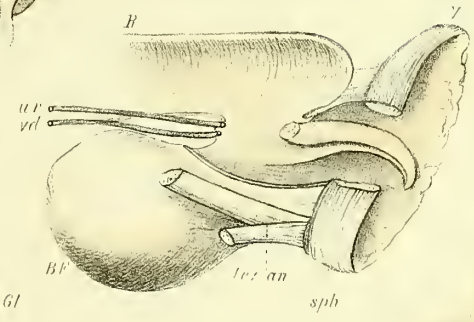

Fig 15

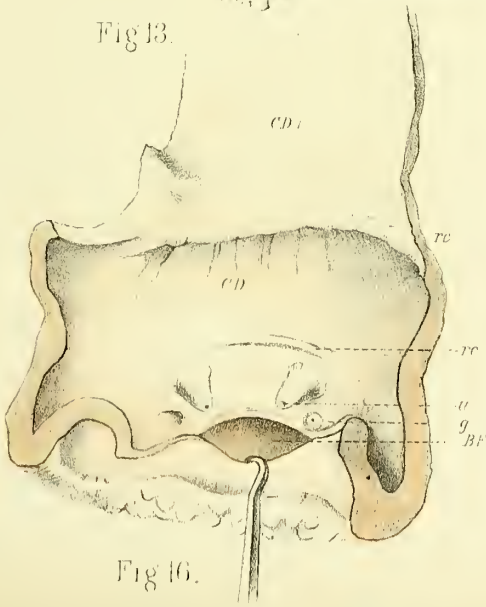

Fig 16.

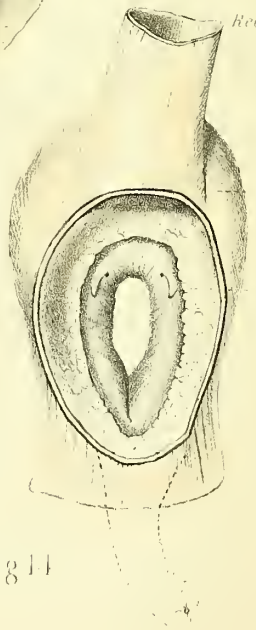

Fig 14


OF SURGEONS OF ENGLAND
18 OCT 89
LIBRARY

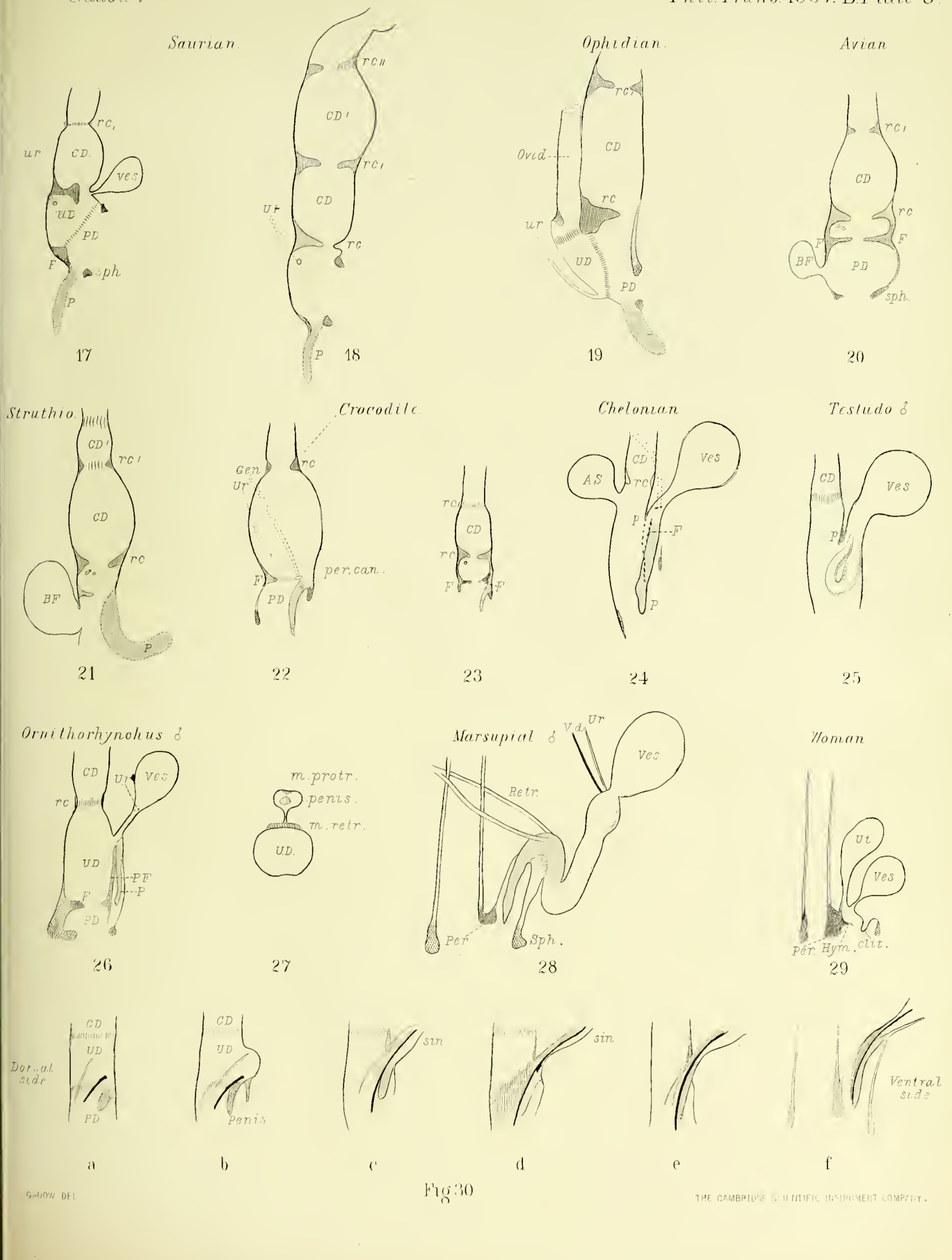

Fig 30


OF SURGEONS OF ENGLAND
OCT 89